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Variation in morphology, life history and ecology of cisco in Great Bear Lake, Northwest Territories, Canada

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Foreword

This series documents the scientific basis for the evaluation of aquatic resources and ecosystems in Canada. As such, it addresses the issues of the day in the time frames required and the documents it contains are not intended as definitive statements on the subjects addressed but rather as progress reports on ongoing investigations.

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ABSTRACT

Historical reports indicate that more than one form of cisco may occur in Great Bear Lake – *Coregonus artedi* and possibly *C. sardinella*. More recent depth-stratified sampling of cisco concurs with earlier studies and includes what may be two or more forms or species. Based on preliminary results, cisco captured in deeper waters of Great Bear Lake showed characteristics that are consistent with those described for Shortjaw Cisco (*C. zenithicus*) including shorter, fewer and more widely spaced gillrakers, lighter paired fins and a diet consisting mainly of *Mysis diluviana*. Other characteristics such as longer paired fins and greater body depth were not consistent with *C. zenithicus*, but are often associated with adaptations to vertically migrating in deeper water and have been noted in other deepwater coregonids such as *Coregonus kiyi*. Cisco from shallow habitats had characteristics typical of *C. artedi* including a more streamlined body, moderately pigmented paired fins, longer more numerous gillrakers and a diet dominated by smaller zooplankton. Deep- and shallow-water cisco were also found to differ in their life history traits, with the deep-water cisco being smaller, later maturing and slower growing than their shallow-water counterparts. In addition to variation by depth, we also observed consistent variation among geographically separated populations within deep- and shallow-water types that may, in part, be due to phenotypic plasticity of morphological traits in response to other habitat differences among lake areas. With the exception of Great Bear Lake, *C. zenithicus* or a *C. zenthicus*-like form of cisco has been reported from most of the remnant proglacial Great Lakes in North America running from the Laurentian Great Lakes northwest to Great Slave Lake. Thus our findings may represent a northern range extension for this particular form or species and certainly represents the first comprehensive account of distinct cisco ecotypes within Great Bear Lake.

Variation de la morphologie, du cycle biologique et de l'écologie du cisco dans le Grand lac de l'Ours aux Territoires du Nord-Ouest, Canada

RÉSUMÉ

Des rapports historiques indiquent que plus d'une forme de cisco pourrait être présente dans le Grand lac de l'Ours : le *Coregonus artedi* et, peut-être, le *C. sardinella*. Un échantillonnage plus récent des ciscos, relevés par couches de profondeur, corrobore les études précédentes et a recensé ce qui pourrait être deux formes ou plus de l'espèce. Selon les résultats préliminaires, les ciscos capturés dans les eaux profondes du Grand lac de l'Ours présentent des caractéristiques qui correspondent aux descriptions du cisco à mâchoires égales (*C. zenithicus*), notamment des branchicténies plus courtes, moins nombreuses et plus espacées, des nageoires paires plus légères et une diète composée principalement de *Mysis diluviana*. D'autres caractéristiques, dont des nageoires paires plus longues et une épaisseur corporelle plus importante, ne correspondaient pas à celles du *C. zenithicus*, mais sont souvent associées à une adaptation à une migration verticale vers des eaux plus profondes et ont été constatées chez d'autres corégonidés d'eau profonde, comme le *Coregonus kiyi*. Les ciscos des habitats peu profonds possèdent des caractéristiques typiques du *C. artedi*, y compris un corps plus effilé, des nageoires paires à pigmentation moyenne, des branchicténies plus longues et plus nombreuses, et une diète composée surtout de petit zooplancton. Les auteurs ont également constaté que les ciscos relevés en eau profonde et en eau peu profonde différaient sur le plan des caractéristiques du cycle biologique : le cisco d'eau profonde était plus petit, arrivait à maturité plus tard et grandissait moins vite que son homologue des petits fonds. En plus des variations relatives à la profondeur, les auteurs ont constaté des variations constantes parmi les populations séparées géographiquement à l'intérieur des types d'eau profonde et d'eau peu profonde. Ces variations pourraient, en partie, être dues à la plasticité phénotypique des caractéristiques morphologies en réponse à d'autres différences d'habitat dans les différents secteurs du lac. À l'exception du Grand lac de l'Ours, le *C. zenithicus*, ou une forme de cisco similaire à ce dernier, a été recensé dans la plupart des grands lacs proglaciaires résiduels en Amérique du Nord, des Grands Lacs laurentiens jusqu'au Grand lac des Esclaves, au nord-ouest. Ainsi, les constatations des auteurs pourraient représenter une extension vers le nord de la portée de cette forme particulière de l'espèce. Elles sont assurément le premier recensement de l'existence de différents écotypes de ciscos dans le Grand lac de l'Ours.

INTRODUCTION

Adaptive radiation and the development of high levels of intraspecific phenotypic diversity are common features of fishes, particularly salmonids in recently deglaciated areas and are thought to be related to high intraspecific competition and niche availability in these regions (Robinson and Schluter 2000; Robinson and Parsons 2002; Bernatchez 2004). Frequently, parallel patterns of diversification or the development of sympatric morphologically distinct types can occur across different systems as well as across species (e.g., Skulason and Smith 1995; Pigeon et al. 1997; Eshenroder et al. 1999). This phenotypic convergence, together with other complicating factors, such as phenotypic plasticity, past colonization from multiple glacial refugia (Bernatchez and Wilson 1998) and the potential for hybridization among different species or types, has made it particularly challenging to understand the evolutionary history and resolve the taxonomy for a number of species complexes (e.g., chars [*Salvelinus*], Reist et al. 1997; Crane et al. 1994; sticklebacks [*Gasterosteus*], Lavin and McPhail 1986; Colosimo et al. 2005; sculpins [Cottoidei] Sideleva 1994). Ciscoes (*Coregonus spp.*) in particular are characterized by exceptional intraspecific variability across their range with respect to morphology, life history and ecology (e.g., Koelz 1929; Dymond 1943; McPhail and Lindsey 1970; Clarke 1973; Steinhiber et al. 2002; Muir et al. 2011; Vecsei et al. 2012) resulting in a high degree of taxonomic uncertainty within this group.

The Shortjaw Cisco, *Coregonus zenithicus*, is one of several closely related species in the cisco complex (McPhail and Lindsey 1970). It was originally described from the Laurentian Great Lakes by Jordan and Evermann (1909). Unlike several other cisco species thought to be endemic to the Great Lakes, *C. zenithicus* as well as *C. artedi* (Cisco, formerly Lake Cisco) were thought to be more widespread and hypothesized to be the primary postglacial colonizing cisco species in North America (Koelz 1929; Smith and Todd 1984). Subsequent genetic studies, however, challenge the idea that all Shortjaw Cisco are a monophyletic species, and show that they frequently have closer genetic relationships to other cisco species or forms within the same lake, rather than to other Shortjaw Cisco populations (Reed et al. 1998; Turgeon and Bernatchez 2001a, b, 2003). Although Shortjaw Cisco morphology can vary widely across their range, they are generally distinguished from Cisco by fewer (32–46) and shorter gillrakers, lower jaw included or even with the upper jaw, a steeper premaxillary angle, lighter coloured ventral area and shorter paired fins (Scott and Crossman 1973, Todd and Smith 1980). Shortjaw Cisco are typically found to inhabit deeper waters (Todd 2002; Nauman 2008; Bunnel et al. 2012; Pratt 2012) where they feed mainly on the opossum shrimp, *Mysis diluviana*[1] and the amphipod, *Diporeia hoyi* (Scott and Crossman 1973; Steinhilber et al. 2002).

With declines in the Laurentian Great Lakes populations, there is an interest in learning more about other potential inland populations of *C. zenithicus* and understanding their taxonomic relationships to those of the Laurentian Great Lakes populations. Great Bear Lake in particular has been highlighted as a location where there is a need for more information on the cisco diversity to help inform decisions by COSEWIC (Committee on the Status of Endangered Wildlife in Canada) (Shortjaw Cisco Recovery Team 2005). With the exception of Great Bear Lake, Shortjaw Cisco or a shortjaw-like cisco morphotype have been reported in most of the remnant proglacial Great Lakes in North America running from the Laurentian Great Lakes

[1] *Mysis relicta* has been shown to be a species complex composed of four taxa; that present in central North American Great Lakes is *M. diluviana*. *M. segerstralei* is distributed in the circumpolar coastal Arctic and may have penetrated inland to Great Bear Lake. Until this is resolved, *M. diluviana* will be used herein.

northwest to Great Slave Lake (Koelz 1929; McPhail and Lindsay 1970; Clarke 1973; Todd and Smith 1980; Houston 1988; Todd and Steinhilber 2002; Vecsei et al. 2012) (Figure 1). Although recent studies of Lake Trout (*Salvelinus namaycush*) in Great Bear Lake have revealed high levels of diversity in this species (Blackie et al. 2003; Alfonso 2004; Chavarie et al. 2013), to date there has been very little research examining the diversity of ciscoes in Great Bear Lake. Great Bear Lake, the northernmost in the string of remnant proglacial lakes, is the only Great Lake within North America that has not been commercially fished or ecologically altered through other mechanisms such as non-indigenous species introductions. It therefore provides an ideal system for studying patterns and mechanisms of intraspecific diversification and speciation in a natural setting.

Cisco were first noted in Great Bear Lake and identified as *Coregonus lucidus* in the early 1800s by Richardson (1836). It was later suggested, based on body measurements and counts that these were similar to *C. artedi* (Gilbert 1895) or *Leucichthys artedi* (Dymond 1943). Although the generic names *Leucichthys* and *Coregonus* (as well as *Argyrosomus*) have been used interchangeably in the past, McPhail and Lindsey (1970) recommended the use of a single generic name (*Coregonus*) for all cisco species, and suggested that a number of species including *C. lucidus* (Richardson) were synonymous with *C. artedi*. Since this time cisco in Great Bear Lake have been collectively referred to as *C. artedi*.

Early studies on Great Bear Lake indicated the possible existence of more than one morphotype of cisco. Kennedy (1949) suggested the possible existence of a dwarf form of cisco based on a single specimen which was observed to mature at a smaller size (101.2 mm) than other cisco in their samples. Kennedy (1953) also noted differences in the morphology of ciscoes from different arms (Keith and McTavish) of Great Bear Lake for several characters including: head length and depth, maxillary length, caudal peduncle length and depth, body depth and fin lengths, but suggested that these differences were most likely due to environmental differences between lake arms. It was concluded that all cisco were *C. artedi* based on comparisons with counts and measurements provided by Dymond (1943), although McPhail and Lindsey (1970) cautioned that in some cases a second form or morphotype in these northern lakes may be part of the *C. sardinella* complex.

Kennedy (1949) also examined the distribution, demography and diet of coregonines, including ciscoes in Great Bear Lake. The majority of ciscoes were captured in the Keith Arm area near the outlet of the Great Bear River, but the presence of populations in the eastern McTavish Arm area was also noted. Ciscoes were mainly captured in bays devoid of vegetation and it was suggested that they avoid extremely oligotrophic conditions of the open lake, however, it is not clear how extensively the latter was sampled. Cisco were found to feed mainly on small plankton (unidentified) and to a lesser extent on *Mysis diluviana*, chironomids and terrestrial insects.

The only other studies that have included the collection of cisco in Great Bear Lake were by Johnson (1975a) and Roberge and Dunn (1988). Johnson (1975a) captured very few cisco (0.28% of total catch) probably due to the fact that he only sampled with large mesh gillnets of sizes (114 and 140 mm) in which cisco are rarely captured (K. Howland, personal observation). Although he did not provide any data directly on cisco, he did show that they were prevalent in the diets of Lake Trout. Roberge and Dunn (1988) only reported catch rates, which were relatively low for cisco in all areas with the exception of McVicar Arm.

More recent research activities by DFO, largely focused on Lake Trout assessment, have provided an opportunity for the complementary collection of depth-stratified cisco samples thus allowing for a more in-depth examination of the taxonomy and ecology of this species within Great Bear Lake. In this study our objectives were to: 1) examine the morphological, meristic,

life history and dietary characteristics of ciscoes from Great Bear Lake to test the hypothesis that there are multiple forms/species including Shortjaw Cisco; and 2) compare ciscoes from Great Bear Lake with morphs/species previously identified in other lakes to provide information that will help address broader questions regarding the taxonomy of Shortjaw Cisco and the cisco complex.

METHODS

STUDY AREA

Great Bear Lake (Figure 2) is the fourth largest lake in North America, and the largest lake entirely within Canada, with a surface area of 31,153 km^2 (Johnson 1975b). The lake has five arms (Keith, Smith, Dease, McTavish, and McVicar) radiating from a large central basin. These arms differ substantially with respect to their bathymetry, the surrounding geology, and the ecozone characteristics (Auld and Kershaw 2005). Its physical characteristics are more similar to lakes of the arctic islands rather than the mainland of Canada (Johnson 1975b). Great Bear Lake is cold monomictic and essentially isothermal due to the short open water season and large volume of water. Surface water temperatures range from 4–5°C over the deepest areas of the lake to up to15°C in sheltered areas during the time of maximum heat input in August (Johnson 1975b; Rao et al. 2012). The lake is deep (mean depth 90 m, maximum depth 446 m) and highly oligotrophic (Johnson 1975b).

Productivity is low as indicated by high secchi depths (up to 30 m) and the low abundance of zooplankton (Johnson 1975a, b; Moore 1981). Great Bear Lake is characterized by an unusually low number of fish species (only 12 regularly occurring) considering its size (Johnson 1975a). The low productivity of this system is believed to result from the combination of cold temperatures and low nutrient input due to the relatively small catchment basin of insoluble rock (Johnson 1975b). Lake Trout is the most abundant large-bodied fish species, followed by ciscoes, *Coregonus* spp., an important dietary item for Lake Trout (Howland et al. 2008).

The lake and its fisheries have remained relatively isolated due to a lack of year-round road access. Deline (formerly Fort Franklin), a Dene community of approximately 650 people located at the south end of Keith Arm, is the only permanent settlement on the lake (Auld and Kershaw 2005). There has never been a commercial fishery on Great Bear Lake, with the exception of a limited fishery to supply the needs of other communities and itinerant anglers in the region (Clarke et al. 1989). However, Great Bear Lake represents one of the two major sport fisheries for Lake Trout in the Canadian north (the other is located in the east arm of Great Slave Lake) (McCart and den Beste 1979). Historically subsistence fisheries captured large quantities of fish (mainly Lake Whitefish, *Coregonus clupeaformis*, and cisco) as food for sled dogs, but with the increased use of snowmobiles and the move away from traditional ways of living there has been a decrease in the amount of fish required to feed dogs (Crawford 1989, Stewart 1996). Fishing, however, still remains an important part of the Dene culture and provides an essential source of protein, with the Lake Trout being the main harvested species in recent years (Stewart 1996; Bayha and Snortland 2002, 2004, 2006).

FISH COLLECTION

All cisco were captured using bottom-set multi-mesh experimental gillnets in mesh sizes ranging from 25.4–101.6 mm typically fished over a 24 hour period within the summer season (mid-July to late August). Samples were collected from two depth zones: 1) less than 50 m (hereafter referred to as shallow), hypothesized to correspond to typical *C. artedi* habitat; and 2) 50–100 m (hereafter referred to as deep), hypothesized to correspond to typical *C. zenithicus* habitat (e.g.,

Nauman 2008; Bunnel et al. 2012; Pratt 2012). All samples were individually placed in plastic bags and stored frozen (-20°C) prior to lab processing. In this paper we focus on data from samples collected in two geographically distinct basins of the lake, the Keith Arm area (2007 & 2008) and the Dease Arm area (2010) (Figure 2) where we had good representation and sample sizes from both shallow- (n = 329 Keith Arm, n = 85 Dease Arm) and deep-water habitats (n = 199 Keith Arm, n = 217 Dease Arm).

MORPHOMETRIC AND MERISTIC CHARACTERS

Twenty-two morphometric measures and 7 meristic counts were taken for each specimen according to Vuorinen et al. (1993); additionally premaxillary angle (PMA) was measured according to Clarke (1973) (Figure 3). With the exception of the premaxillary angle (measured to the nearest 1 degree using a compass) and standard length (measured to the nearest 1 mm using a measuring board), all morphometric characters were measured to the nearest 0.1 mm using digital calipers.

For all morphometric and meristic analyses we only included individuals with a standard length of greater than 100 mm, the smallest size at which we observed mature fish. All variables were initially examined using a Pearson correlation matrix to determine relationships to body size and test for effects of allometry. No significant correlations were observed between meristic characters and standard length of samples. However, all morphometric variables, with the exception of premaxillary angle were strongly linearly correlated (correlation coefficient >0.8) with standard length. Therefore, all absolute morphometric measurements (with the exception of premaxillary angle) were initially transformed to size-independent shape variables following the approach recommended by Reist (1986). Since significant heterogeneity was found among slopes of regressions of the different variables on standard length for samples collected from individual populations and depth zones/habitats (e.g., Keith Arm-Shallow, Keith Arm-Deep, Dease Arm-Shallow, Dease Arm-Deep) (Analysis of Covariance (ANCOVA), $P>0.05$), we used the common-within groups method to compute size-adjusted variables (Reist 1986).

A Pearson correlation matrix with all size-adjusted variables as well as standard length was then re-calculated to check if the data transformation was effective in removing the effect of size and to test for correlations (redundancy) among variables. The standardized measurements were not strongly correlated with standard length or with each other (correlation coefficients <0.8) indicating the size effect had been successfully removed with the transformation and it was not necessary to remove any redundant variables for further analyses.

A one-way analysis of variance (ANOVA) with post hoc Tukey's test was used to determine whether there were any statistically significant differences between the sample collection sites for each character. Morphometric and meristic characters were used separately in all follow-up multivariate analyses since these variables are different statistically (the former are continuous while the latter are discrete). A discriminant function analysis (DFA) was first run to test how well individuals fit into *a priori* groupings and based on capture location (lake-arm) and habitat preference (based on depth). Similarly, a second DFA was run based on groupings generated using a hierarchical cluster analysis to see how well these aligned with original *a priori* groups. Ward's method with squared Euclidean distance was used to evaluate the optimal number of clusters. This method uses an ANOVA approach to determine the number of clusters that minimizes the total sum of squared deviations from the mean of each cluster. Once the optimal number of clusters was determined the K means procedure was used to conduct cluster assignments.

All discriminant function scores were plotted to visualize relationships between the groups along the first and second canonical axes. The classification success rate was evaluated based on the

percentage of individuals correctly assigned into original sample groups using a cross-validation procedure. Discriminant loadings were used to assess relative importance of individual variables in discriminating among groups. All statistical analyses were performed using SPSS v11.0.1.

DEMOGRAPHIC CHARACTERS

In addition to standard length (described above), specimens were sampled for body weight (to the nearest 1 g), age structures (otoliths), sex, maturity, and gonad weight (to the nearest 0.1 g).

All aging was done at the Winnipeg Freshwater Institute fish aging lab using standardized protocols. Otoliths were removed, cleaned and stored dry in coin envelopes. Otoliths were prepared for reading using a modified version of the "break and burn" technique (Chilton and Beamish 1982). One otolith from each pair was broken in transverse cross-section through the nucleus by repeatedly scoring the surface with a scalpel blade. The broken surface on both halves of the otolith was then polished smooth using 30 micron lapping film mounted on a grinding wheel. The polished surfaces were burned in an alcohol flame to produce a distinct banding pattern. Otoliths were mounted in plasticine and immersed in water to improve the contrast between growth zones. Ages were read using a dissecting microscope at 20–40X magnification. An annulus was considered to consist of a wide, light, opaque zone and an adjacent narrow, dark, translucent, hyaline zone, as seen when the burned otolith was viewed under reflected light (Jearld 1983; Secor et al. 1992).

When estimating ages, a readability factor was assigned on a five-level scale ranging from good to poor (Table 1). Samples from each location and year were also tested using the standard aging lab procedures for quality assurance and quality control (QA/QC). After the first reader has completed age reads for a sample, a second reader independently re-ages a randomly selected sub-sample (15%) to ensure that age differences are within a predetermined range considered to be acceptable. All samples included in this study were ranked within the top 3 levels of the readability scale (good, fairly good or fair) and passed the QA/QC test.

Stage of maturity (immature versus mature) was determined by examining plots (by population-depth category) of gonadosomatic indices and length and age for obvious discontinuities. Maturity was also qualitatively assessed in the field based on appearance, however these data were considered less reliable due to the high likelihood of resting mature fish which can often be confused with immature fish.

DIET

Samples of cisco from the Keith Arm of Great Bear Lake that were analyzed for morphometric and meristic differences (see results below), demonstrated the presence of at least two morphotypes that appear to be strongly associated with the shallow (<50 m) and deep (≥50 m) habitats that were sampled. Samples from the shallow and deep habitats from Keith (shallow n = 30; deep n = 10) and Dease (shallow n = 10; deep n = 10) arms that were clearly morphologically different were randomly selected for stomach content, stable isotope and fatty acids analysis. The objective of these analyses was to compare the trophic ecology of the shallow- and deep-water morphotypes by: 1) identifying prey items that have been recently consumed by examining stomach contents, 2) characterizing the long-term diet of the morphotypes using stable isotopes and fatty acids, 3) examine the trophic position (isotopes) and 4) sources of fatty acids by comparing with results from important prey items, and 5) determine whether morphological differences may be related to diet specialization.

Stomach contents

The stomach was removed from each cisco and the contents were examined under a dissecting microscope. The majority of prey items were enumerated and identified to Order while some were identified to Family and Genus. The diets of deep- and shallow-water morphotypes were summarized by calculating the percent frequency of occurrence (% individuals with the diet item) (% O*i*) and percent total of diet items (based on the total sum of enumerated diet items) (% N*i*). Using % O*i* and % N*i*, the relative importance index (RI) was calculated for each diet item (*i*) (George and Hadley 1979):

$$RI_i = 100 \times AI_i / \sum_{i=1}^{n} AI_i$$

where AI_i is the absolute importance of prey item *i* (% O*i* + % N*i*). The RI_i is modified from George and Hadley (1979) who calculate RI_i by using the sum of % O*i*, % N*i* and percent total mass from each diet item. Weights from the cisco prey were not available. Dietary overlap between deep- and shallow-water morphotypes was quantified using Horn's index of dietary overlap (R_0) (Horn 1966):

$$R_0 = \frac{\sum(P_{ij} + P_{ik}) \log(P_{ij} + P_{ik}) - \sum P_{ij} \log P_{ij} - \sum P_{ik} \log P_{ik}}{2\log 2}$$

where R_0 is the index of dietary overlap between populations j and k (e.g., deep- and shallow-water morphotypes), P_{ij} is the proportion of resource i (prey item) of total resources used by population j, and P_{ik} is the proportion of resource i of total resources used by population k. R_0 is 0 when populations have no overlap and 1 when populations have identical prey abundance and composition.

Stable isotopes

A piece of muscle from the anterior dorsal region of the body was removed from each frozen cisco and freeze-dried for approximately 48 hours (Keith Arm shallow morph n = 30 and deep morph n =10; Dease Arm shallow morph n = 10 and deep morph n = 10). Invertebrate samples (i.e., copepods, *Mysis diluviana*, Hymenoptera, Trichoptera and Amphipoda) obtained from the stomach contents of Lake Trout were also freeze dried. Individual fish, and composite samples [copepods (n = 2), *Mysis diluviana* (n = 2), Hymenoptera (n = 6), Trichoptera (n = 3), Amphipoda (n = 1)] were homogenized and sent to the Stable Isotope Hydrology and Ecology Laboratory (National Water Research Institute, Environment Canada) for analysis of its carbon and nitrogen isotope ratios. A 1 mg sub-sample was encapsulated in a 5 x 8 mm tin capsule and analyzed with a Europa Scientific ANCA G/S/L elemental analyzer coupled to a Tracer/20 mass spectrometer. Egg albumen was periodically used as a reference sample in order to measure the level of error in isotopic results. The results are reported as δ values and ‰ deviations from the international reference standards (i.e., PeeDee Belemnite for $\delta^{13}C$ and atmospheric nitrogen for $\delta^{15}N$) and calculated as:

$$\delta^{13}C \text{ or } \delta^{15}N = [(R_{SAMPLE} / R_{STANDARD}) - 1] \times 1000$$

where $R = {}^{13}C/{}^{12}C$ or ${}^{15}N/{}^{14}N$.

The C:N ratio from all samples were <3.5, indicating that $\delta^{13}C$ did not have to be adjusted because of high lipid content (Post et al. 2007).

Fatty acids

The same batch of tissues freeze dried for isotopic analyses was used for fatty acids analysis. Lipids were extracted from 0.25 g of freeze dried muscle with 2:1 chloroform-methanol containing 0.01% butylated hydroxytoluene (BHT) (v/v/w) (Folch et al. 1957). The lipid phase was filtered, collected, and dried with anhydrous sodium sulphate and evaporated under nitrogen to obtain the total lipid weight. The extracted lipid was used to prepare the fatty acid methyl esters (FAME) by transesterification with Hilditch reagent (0.5 N H_2SO_4 in methanol) (Morrison and Smith 1964). The samples were heated for 1 h at 100°C. Gas chromatographic (GC) analysis was performed on an Agilent Technologies 7890N GC equipped with a 30 m J&W DB-23 column (0.25 mm I.D; 0.15 µm film thickness). The GC was coupled to a Flame Ionization Detector (FID) operating at 350°C. Hydrogen was used as carrier gas flowing at 1.25 mLs/min for 14 minutes and ramped to 2.5 mLs/min for 5 minutes. The split/splitless injector was heated to 260°C and run in splitless mode. The oven program was as follows: 60°C for 0.66 min; 22.82°C/min to 165°C with a 1.97 min hold; 4.56°C/min to 174°C and 7.61°C/min to 200°C with a 6 min hold. Peaks were quantified using Agilent Technologies ChemStation software Fatty acid standards were obtained from Supelco (37 component FAME mix) and Nuchek (54 component mix GLC-463). Every 10th sample was run in duplicate to monitor GC performance and the consistency with which chromatograms were interpreted. The GC detector was calibrated with 50, 100, 200 and 380 ng/ul standards made by diluting the Supelco 37 component FAME mix. These calibration standards were run in duplicate once during each sample run. Samples were diluted and re-run if required to ensure they fell within the flame ionization detector's linear range as determined by the calibration curve. Fatty acid standards (50 ng/ul, Supelco and Nuchek GLC-463) were run every 10th sample during a sample run to monitor GC performance/detector drift and two blanks were run with the sample set. Seventy-three FAME were identified via retention time and known standard mixtures and are reported as percent of total fatty acid. Each fatty acid is described using the shorthand nomenclature of A:Bn-X, where A represents the number of carbon atoms, B the number of double bonds and X the position of the double bond closest to the terminal methyl group. Data were examined using a discriminant function analysis in order to determine if fatty acids were significantly different between morphotypes from both arms of the lake.

RESULTS

MORPHOMETRICS AND MERISTICS

We found that mean (± standard deviation) and modal gillraker numbers were lower in cisco from deepwater habitats but that the distributions between deep- and shallow-caught cisco overlapped, particularly in the Dease Arm area (Table 2) (Figure 4). Although some morphological studies of ciscoes group individuals for analysis on the basis of gillraker number (e.g., Steinhilber et al. 2002), we chose to test groupings based on population and depth of capture since gillraker numbers were not clearly bimodal.

A priori population-depth zone groupings

Morphometric

Univariate statistics showed that with the exception of maxillary width ($P = 0.73$) and adipose length ($P = 0.05$), all morphometric variables were significantly different between population-depth zone groupings ($P<0.01$).

The *a priori* groupings based on population and depth of capture were well supported by the DFA (Wilks' Lambda 0.039, Chi-square $P<0.0001$) with an overall classification success of

92.2%. The first two axes combined explained 96.2% of the total variability in morphometric characteristics among groups (Figure 5A). Axis 1 mainly separated groups from deep- versus shallow-water habitats, however, differentiation among depth zones was stronger for Keith Arm. Axis 1 had high negative loadings for pre-orbital length, body depth, and pectoral fin length and high positive loadings for caudal peduncle length, caudal peduncle depth and lumbar length (Table 3). Individuals from deep habitats (both Keith and Dease Arm) had greater pre-orbital length, body depth and pectoral fin lengths, and shorter caudal peduncle length, caudal peduncle depth and lumbar length, while those from shallow water in Keith Arm showed the opposite suite of characters. Those from the shallow-water habitat in Dease Arm had more intermediate characters (Figure 5A). Axis 2 mainly separated individuals from the two populations or lake arms within each depth zone with high negative loadings for interorbital width, lower arch length and caudal peduncle length, and high positive loadings for trunk length, dorsal length and gillraker length. Individuals from the Keith Arm area generally had a greater interorbital width, lower arch length and caudal peduncle length and shorter trunk length, dorsal length and gillraker lengths, relative to fish from the Dease Arm area.

The Keith Arm shallow group had the highest proportion of correctly classified individuals (98.4%), followed by the Keith and Dease Arm deep groups (91.1% and 91.7%, respectively) (Table 4). The misclassified Keith Arm deep samples were mainly assigned to either the Dease Arm deep group or the Keith Arm shallow group, while the majority of misclassified Dease Arm deep samples were assigned to the Dease Arm shallow group. The Dease Arm shallow group had the lowest classification success (69%), with the majority of misclassified individuals assigned to the Dease Arm deep group (Table 4).

Meristic

Univariate statistics showed that all meristic variables were significantly different between population-depth zone groupings ($P<0.0001$).

Similar to the above DFA using morphometric data, there was also good support for *a priori* population-depth zone based groups when a DFA was run using meristic variables (Wilks' Lambda 0.162, Chi-square $P<0.0001$), however, overall classification success was lower (81.2 %). The first two axes combined explained 97.3% of the total variability between groups (Figure 5B). Again Axis 1 clearly separated groups from deep- versus shallow-water habitats and had high positive loadings for gillraker number and lateral line scales (Table 3). Individuals from shallow-water habitats generally had higher numbers of gillrakers and lateral line scales than those from deep habitats (Figure 5B), however, some individuals from the Dease Arm shallow-water group did overlap with those from the deep-water group suggesting they had more intermediate characters. Consistent with the morphometric results above, axis 2 mainly separated individuals from the two populations or lake arms within each depth zone with high negative loadings for lateral line scales and high positive loadings for anal and pectoral ray counts (Table 3). Individuals from the Keith Arm population generally had higher anal and pectoral ray counts and a higher number of lateral line scales relative to fish from the Dease Arm area (Figure 5B).

The cross validated classification results from the DFA using meristic variables were generally consistent with those observed with the morphometric variables, however, classification success was proportionally lower in each of the groups (Table 4). The Keith Arm shallow group had the highest success (95.1%) and mis-classified individuals were most often assigned to the Dease Arm shallow group. Keith Arm and Dease Arm deep samples had similar classification success (75.7% and 73.4%, respectively); in contrast to the morphometric results, where mis-classified deep-water individuals were most often assigned to the shallow-water group of the same population, in this case the majority of misclassified samples were assigned to the other deep-

water group. The Dease Arm shallow group had the lowest classification success (52%) with the majority of misclassified samples assigned to either the Keith Arm shallow or Dease Arm deep groups.

Although pigmentation was not included in cluster/DFA analyses, comparisons between the level of fin spotting in cisco from deep- and shallow-water habitats in Keith Arm showed that individuals from deep water had either little or no paired fin pigmentation, whereas those from shallow water had moderate to heavy fin pigmentation (Figure 6). Data on fin coloration were not available for the Dease Arm sample. Ventral coloration was light tan or white for all individuals in both populations.

Hierarchical cluster analysis groupings

The results from the cluster analyses align well with the above *a priori* analysis which showed that although the Dease Arm shallow group was distinct (both for morphometric and meristic characters), it had the highest rate of misclassification mainly to the Dease Arm deep and Keith Arm shallow groups suggesting some degree of overlap in characters between these groups. The cluster and *a priori* analyses were also consistent in that for both cases the group containing Keith Arm shallow individuals appeared to be most distinct and have the highest classification success.

The hierarchical cluster analysis using Ward's method suggested 3 clusters to be most likely. The K-means procedure was used to assign individuals to each of these 3 clusters which were then tested using a DFA. Cluster 1 and 3 were predominantly made up of individuals from the deep and shallow habitats in the Keith Arm areas, respectively, indicating marked differences in morphology between these two groups. Cluster 2 was dominated by individuals from the Dease Arm deep habitat (Figures 7A and 7B). The fourth *a priori* group, individuals from the Dease Arm shallow-water habitat, were not distinguished in the cluster analysis, but were grouped together with mainly clusters 1 (predominantly Dease Arm deep) and 3 (predominantly Keith Arm shallow).

Morphometric

The 3 clusters were well supported by the DFA run with morphometric variables (Wilks' Lambda 0.139, Chi-square P<0.0001), however overall classification success was lower (87.7%) than when the analysis was run using *a priori* population-depth zone groups (Figure 7A, Table 5). Cluster 3 (mainly Keith Arm shallow individuals) had the highest classification success (93.3%), followed by clusters 1 and 2 (84% and 81.9%, respectively) (Table 5).

Meristic

Although the DFA run with meristic variables statistically supported the 3 groupings suggested by the hierarchical cluster analysis (Wilks' Lambda 0.277, χ^2 P<0.0001), the results were not as strong, and overall classification success (79.6%) was lower than when the analysis was run with the *a priori* groupings (Figure 7A, Table 5). Similar to the morphometric results, cluster 3 had the highest classification success, followed by clusters 1 and 2 (54.7% and 80.8%, respectively) (Table 5).

DEMOGRAPHICS

Because the overall statistical support and classification success was higher based on *a priori* population-depth zone based groups, we maintained these 4 groups for all subsequent demographic and diet analyses rather than reducing the total number of groups to 3 as suggested by the hierarchical cluster analysis.

Comparisons of mean size-at-age between sexes in this study showed no consistent differences between males and females. Similarly, previous studies of cisco demographics in this system showed no difference between males and females for size- and age-related characteristics (Kennedy 1949). Based on this information we chose to pool males and females for our size-at-age analyses. Comparison of size-at-age among population-depth zone groups showed that individuals from deep-water habitats had lower sizes-at-age and reached smaller asymptotic sizes (approximately 160 mm) than did individuals from shallow-water habitats (asymptotic size approximately 300 mm) regardless of population (Figure 8). There were no differences in size-at-age among populations within each depth habitat.

Comparisons of size- and age-at-maturity among population-depth zone groups showed that cisco from deep-water habitats generally mature at smaller sizes (size at 50% maturity 120–129 mm) (Figure 9A) and older ages (age at 50% maturity 6–7 years, Figure 9B) than those from shallow-water habitat (size at 50% maturity 180–220 mm; age at 50% maturity 4–5 years). Although size- and age-at-maturity generally appear to be similar among populations within a given depth habitat, size-at-maturity does appear to be smaller in the Dease Arm as compared to Keith Arm shallow water group (Figure 9A).

DIET

Stomach contents

The stomach contents of cisco from Keith Arm consisted of 18 taxa, predominantly comprised of invertebrates (Table 6). The deep-water group had a lower diversity of prey items (n = 8) compared to the shallow-water group (n = 16). The most abundant diet item in the deep-water group was the crustacean *Mysis diluviana*, which had an RI value of 54.3%, followed by adult Dipterans (20.5%) (Figure 9A). The remaining items were low in abundance with RI's of ≤5%, which included fish remains and invertebrates such as Coeloptera and Hymenoptera. The shallow-water group from Keith Arm fed mainly on copepods (RI = 32.5%), adult Trichopterans (RI = 19.9%) and adult Dipterans (RI = 13.7%). The greater diversity of diet items found in the shallow-water group is a result of the consumption of a greater number of invertebrates from the terrestrial environment compared to the deep-water group, which included species from the Orders Lepidoptera, Megalopetra and Hemiptera (Figure 9A). Very little dietary overlap was detected between shallow-water and deep-water groups from Keith Arm as R_0 was equal to 0.104.

The stomach contents of ciscoes from Dease Arm consisted of 12 taxa, and similar to results from Keith Arm, fewer taxa were observed in the deep-water group (n = 7) compared to the shallow-water group (n = 10) (Table 6). The most abundant prey item found in stomachs was *Mysis diluviana* (RI = 39.1%) and copepods (RI = 43%) in deep- and shallow-water groups, respectively (Figure 10B). A greater number of terrestrial invertebrates were detected in the shallow-water group from Dease Arm. Very little dietary overlap was detected between shallow-water and deep-water groups from Dease Arm as R_0 was equal to 0.02.

Stable isotopes

The $\delta^{13}C$ of the deep-water cisco group from Keith Arm ranged between -24.98 and -26.66 (mean = -25.73‰), while the $\delta^{13}C$ of the shallow-water group ranged between 24.98 and -27.37 and (mean = -25.95‰), with no statistically significant difference between both groups (ANOVA $F = 1.2$, d.f. = 1, 38, $p = 0.3$) (Figures 11 and 12). In contrast, $\delta^{15}N$ values differed significantly between the deep-water (range = 9.33 and 10.47‰, mean = 10.04‰) and shallow-water (range = 7.76 and 10.18‰, mean = 8.89‰) groups in Keith Arm as the deep-water group was more enriched in $\delta^{15}N$ (Figures 11 and 12) (ANOVA $F = 38.6$, d.f. = 1, 38, $p > 0.001$). In Dease Arm,

there was considerable overlap in $\delta^{13}C$ between deep- (range = -27.15 and -28.75‰, mean = -27.68‰) and shallow-water (range = -26.16 and -29.57‰, mean = -27.62) morphs, with no statistically significant differences observed (ANOVA F = 0.024, d.f. = 1, 18, p = 0.8) (Figures 11 and 12). Similarly, no significant differences in $\delta^{15}N$ were detected between deep (range = 9.56 to 10.64‰, mean = 10.11 ‰) and shallow morphs (range = 9.51 to 10.34‰, mean = 9.85 ‰) (ANOVA F = 3.26, d.f. = 1, 18, p = 0.08) in Dease Arm. Regardless of group, the $\delta^{13}C$ of cisco from Dease Arm was more depleted than those from Keith Arm while the $\delta^{15}N$ values among deep water Dease/Keith and shallow-water Dease ciscoes were very similar. The average $\delta^{15}N$ of cisco was enriched compared to all invertebrates (Figure 12). $\delta^{13}C$ of copepods and *Mysis diluviana*, were depleted compared to cisco. Both isotopes from copepods were depleted relative *to Mysis diluviana*. The $\delta^{13}C$ of Trichoptera and Hymenoptera were enriched and depleted, respectively, compared to cisco.

Fatty acids

Fatty acids were examined for cisco from Keith Arm and Dease Arm along with *Mysis diluviana*, Trichoptera and Amphipoda, the only prey items for which we had data available for this document (Figures 13 and 14). Out of the 73 fatty acids analyzed, 6 were omitted because most of the values (approximately 95%) were 0. The average difference between replicates among fatty acids was 0.02, indicating low variability. Significantly different fatty acids between deep- and shallow-water groups are listed in Table 7. The abundant fatty acids (>1%) that were considerably different between morphs were 14:0, 16:0, 18:0, 16:1n7, 18:1n7, 18:1n9c, 18:3n3, 20:5n3, 22:5n6, 22:5n3c, and 22:6n3. The DFA comparing fatty acid among the four population-depth zone groups of cisco was highly significant (Wilks' lambda <0.001, $X^2(162) = 393.72$, p< 0.001), with the first and second functions accounting for 61.1% and 21.3% of the variance, respectively (Figure 15). Not only does the DFA reveal that fatty acids between shallow- and deep-water groups are different, but also that the groups from both arms are different (Figure 15). The deep-water groups from Keith and Dease had a more similar fatty acid composition to each other than with the respective shallow-water groups from the same arm.

DISCUSSION

MORPHOLOGICAL GROUPINGS

The multivariate analyses of morphometric and meristic data using both *a priori* population-depth zone groupings and groups based on hierarchical cluster analysis clearly support the hypothesis that multiple distinct forms of cisco occur in Great Bear Lake. These morphological groups were most clearly distinguished based on the depth of capture (shallow versus deep), a pattern that is consistent with observations of cisco in a number of other proglacial lakes (e.g., Clarke 1973; Todd and Steinhiber 2002; Nauman 2008; Muir et al. 2011; Vecsei et al. 2012). Our analyses also indicate further subdivision of individuals from shallow and deep habitats based on population (lake arm).

Several of the characters that distinguished deep from shallow groups in both the Keith and Dease Arm populations appear to be functionally related to differences in feeding and vertical migration. For example, deep-water groups in both lake arms had greater body depth and paired fin lengths and a reduced caudal peduncle area (length and width). A greater body depth is often associated with increased positive buoyancy reducing the amount of swimming required to vertically migrate up through the water column, while longer paired fins are frequently utilized by vertically migrating species to maintain hydrostatic lift and allow for a more gradual descent during vertical migration (Eshenroder et al. 1999). A reduced caudal peduncle is usually associated with reducing drag during forward movement in pelagic predators (Moyle and Cech

2003), and may suggest that the deep-water forms feed on faster moving prey. Deep-water morphs also had shorter and fewer gillrakers suggesting they feed on larger (and likely faster moving) prey than shallow-water morphs. In contrast shallow morphs had a more streamlined body, moderate fin lengths and longer more numerous gillrakers typically associated with feeding on smaller zooplankton.

Traits that distinguished populations from different lake arms within each depth zone appeared to be less associated with functioning in different depths (e.g., interorbital width, trunk length, and anal and pectoral ray count). These inter-arm morphological trait differences may reflect phenotypic plasticity in response to other habitat differences among lake arms, or possibly reproductive isolation and drift between populations over time.

TROPHIC SPECIALIZATION

The diet analyses based on stomach contents, stable isotopes and fatty acids strongly corroborate the morphological groupings and clearly show that shallow- and deep-water groups occupy different dietary niches. Based on stomach contents, the shallow-water morphs in both Keith and Dease arms feed on a greater number of invertebrate items that are more closely associated with nearshore aquatic habitats. For example, copepods, the most frequent and prevalent prey item for shallow-water morphs, have been shown to be most abundant in nearshore areas (in depths ≤20 m) and less abundant in offshore areas (depths at least ≥40 m) of Great Bear Lake (Johnson 1975a). Shallow-water morphs also had a greater frequency of invertebrates derived from the terrestrial environment, likely from or near the riparian zone, such as adult trichopterans, dipterans and hymenopterans. It should be noted however, that adult trichopterans were absent from the diet of shallow-water cisco from the Dease Arm area and could be related to a mismatch between emergence timing and timing of fish collection. Most terrestrial invertebrates are likely to have been brought into the water by wind, either alive or previously dead. Other dietary items such as adult trichopterans may have been consumed while lying on the surface to deposit eggs or having recently emerged from the aquatic pupae stage. Either way, the presence of terrestrial insects, particularly adult trichopterans, in the diet indicate that shallow-water morphs spend time feeding at the surface as well as within the water column.

In contrast the deep-water morphs in both Keith and Dease Arms fed mainly on *Mysis diluviana* a vertically migrating species typically associated with deeper offshore pelagic habitats. Johnson (1975a) found that *Mysis* density (number/m^2) in Great Bear Lake was relatively low near the surface (5/m^2) and increased with depth, peaking at depths of between 22 and 75 m (22/m^2) and decreasing considerably thereafter (depths ≥60 m). The deep-water morph appears to also consume terrestrial prey which either suggests they opportunistically feed on terrestrial invertebrates that are sinking towards the bottom or that periodically these morphs may feed at the surface or move into shallower areas where the likelihood of encountering terrestrial food sources may be higher.

The higher number of gillrakers in the shallow-water morph, suggestive of feeding on smaller-sized diet items, corresponds with the dietary information which shows that copepods are the most important prey item. The lower number of gillrakers in the deep-water morph suggests that they feed on larger-size prey, compared to the shallow-water morph. *Mysis* are a larger size prey than copepods and in deep-water morphs, these are the most abundant diet item while copepods were not observed.

The stable isotope results for the Keith Arm population generally conformed to what was seen in gut content analyses. The $\delta^{15}N$ of *Mysis* was higher than copepods, and as would be expected, the deep-water form (found to consume mainly *Mysis*) had a significantly higher $\delta^{15}N$ than the

shallow form which mainly fed on copepods. In contrast, no difference in $\delta^{15}N$ was observed between forms in Dease Arm, even though *Mysis* were abundant in the diet of the deep form. The discrepancy in these results is equivocal, and may be a result of different feeding ecologies of *Mysis* in both arms or because of the influence of isotopic signatures from other prey sources that may be more abundant in shallow-water habitats (e.g., cladocera). The carbon isotope results, from both locations, did not show any difference between shallow and deep forms suggesting that the integrated carbon signal from all prey combined does not differ between them. Although one would expect the shallow-water form to have a more depleted $\delta^{13}C$ relative to the deep-water form because copepods are considerably depleted in $\delta^{13}C$, this was not the case. This suggests that the $\delta^{13}C$ from the other invertebrates may be more enriched. For example, trichopterans, which were the second most abundant prey item in the shallow-water form from Keith Arm, were enriched in $\delta^{13}C$.

The fatty acid results were consistent with gut content analyses in that the deep-water cisco showed signals from *Mysis* (e.g., 20:5n3), the main prey item found in their diet. It is difficult to elaborate further due to the lack of fatty acids data for other prey species, particularly copepods. The patterns of variation in the fatty acids also most closely mirrored the results based on morphology, showing clear separation among individuals both in relation to depth as well as by population or lake arm. Interestingly the greatest separation on the first axis of the discriminant function analysis was between individuals from different depth zones as was seen in the morphological analyses. Separation on the second discriminant axis was mainly between populations (lake arms) within each depth zone, suggesting that there are likely differences in energy sources and the base of the food web between different arms of the lake. This is corroborated by the stable isotope results, which show a difference in $\delta^{13}C$ in ciscoes between both arms,suggesting that the sources of carbon absorbed by the prey are different. These observations may in part be explained by the substantial differences in the geology and the ecozones in which each of these lake arms lie (Auld and Kershaw 2005). Keith Arm is the most southerly basin in the lake and is located within the warmer Taiga Plains Ecozone and the Interior Platform Geological Province and would be expected to have higher terrestrial carbon inputs from permafrost and bog habitat, while Dease Arm is the most northerly basin and extends into the colder Southern Arctic Ecozone and the Bear and Arctic Platform Geological Provinces (Auld and Kershaw 2005).

LIFE HISTORY VARIATION

Demographic results clearly show that there are life history differences among ciscoes utilizing different depth zones and dietary resources. Deep-water groups were slower growing and later maturing than the shallow-water types. Shallow-water forms consumed a larger variety of prey from both aquatic (Keith only) and terrestrial habitats, and occupied nearshore habitats that are typically higher in temperature than deep-water forms which may explain the difference in growth rate between the forms. A combination of higher temperature as well as potential higher abundance, capture rate and/or caloric value of prey in the near shore habitat may explain the higher size-at-age (growth rate) of cisco from shallow-water habitats. Differences in size and age at maturity are likely a consequence of differences in growth rates between cisco from different depth zones. Deepwater cisco appear to be delaying maturity to some extent in order to reach what is likely a physiological minimum needed to reproduce. The extremely slow rates of growth in this form may not make it worthwhile to delay maturity longer as the risks of mortality may outweigh any slight gains in reproductive output as a result of increased size at maturity. Conversely, shallow-water cisco grow much faster and are therefore able to mature at much larger sizes and younger ages. Longevity of the two forms appears to be similar, despite differences in age at maturity.

Demographic characters of the shallow forms in this study were consistent with those described for the majority of samples analyzed by Kennedy (1949). They found that 50% maturity was reached at age 6 and at a length of 254–305 mm. The single specimen they suggested to be a dwarf form had a size at maturity (101 mm) in the range of what we observed for the deep-water cisco in this study, however, age at maturity (3 years, ages using scales) was much younger, suggesting that this specimen may represent yet another type of cisco that was not present in our samples. Size-at-age for shallow-water forms in our study also appeared to be consistent with earlier studies by Keller (1949) who found that cisco reached asymptotic sizes at ages 6–7 and at approximately 300 mm.

TAXONOMIC RELATIONSHIPS WITH CISCO IN OTHER SYSTEMS

Much of the morphology, life history and habitat of deep-water cisco in Great Bear Lake is consistent with that of *C. zenithicus* identified in other lakes including shorter, fewer and more widely spaced gillrakers (Table 8), lighter paired fins, and a diet consisting mainly of *Mysis diluviana*, whereas the morphology and habitat of shallow forms align more closely with *C. artedi*. Although gillraker distributions overlapped between deep and shallow forms, the mean number of rakers was significantly lower in the deep-water form and the range was within that observed elsewhere for *C. zenithicus* (Table 8). Shallow-water cisco raker numbers although higher than in the deep-water form, were generally lower than that reported in literature for other populations of *C. artedi*, with the exception of Great Slave Lake (Table 8). The diets and habitats of the deep-water forms in Great Bear Lake were similar to *C. zenithicus* in that they were associated with offshore areas in depths greater than 50 m and fed predominantly on *Mysis*. Although *C. zenithicus* are also reported to feed on *Diporeia* (Scott and Crossman 1973), this prey species does not occur in Great Bear Lake (Johnson 1975a).

Some characteristics such as longer paired fins and greater body depth are not typical of *C. zenithicus*, but are often associated with adaptation to vertically migrating in deeper water and have been noted in other deep-water coregonines such as *C. kiyi* (Eshenroder et al. 1999).

With the exception of Great Bear Lake, *C. zenithicus* or a *C. zenthicus*-like form of cisco has been reported from most of the remnant proglacial Great Lakes in North America running from the Laurentian Great Lakes northwest to Great Slave Lake (Todd 2002). Thus our findings may represent a northern range extension for this particular form or species and certainly represents the first comprehensive account of distinct cisco groups within Great Bear Lake.

RECOMMENDATIONS FOR FURTHER RESEARCH

- Sampling from deeper regions of Great Bear Lake (>100 m).
- Further research into habitat use between groups.
- Detailed examination of the food web in Great Bear Lake, including further work on the stables isotopes and fatty acids of prey species and an improved understanding of the allochthonous input from terrestrial sources around the lake.
- Comprehensive lake-wide analysis of life history and morphological/meristic characteristics of ciscoes.
- Comprehensive comparisons with *C. zenithicus*, *C. artedi*, and possibly other cisco species from other large lakes, particularly from the Laurentian Great Lakes.

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Table 1. Reader confidence index for age estimates.

Confidence Index	Abbreviation (CI)	Qualitative meaning (Pattern clarity)	Quantitative meaning (Repeatability)	Age and Comments examples
Good	G	Pattern is very clear with no interpretation problems	Reader would always get the same age	10+(G), 38+(G)
Fairly good	FG	Pattern is clear with a few easy interpretation problems	Reader would get the same age most of the time for fish < 20 years, within 1 year for fish 20-40 years, etc.	7+(FG), 33+ (FG)
Fair	F	Pattern is fairly clear with some areas presenting easy and moderate interpretation problems	Reader would be within 1 year most of the time for fish < 20 years and 2-3 years for fish 20-40 years, etc.	9+ (F) – 1st year is ???
Fairly poor	FP	Pattern is fairly unclear presenting a number of difficult interpretation problems	Reader would be within 2-3 years most of time for fish < 20 years and 4-5 years for fish 20-40 years, etc.	19+(FP) – may be 1 more between 3 and 4; outer rings are close together and weak
Poor	P	Pattern is very unclear presenting significant interpretation problems	Reader has little confidence in repeatability of age within 5-10 years, or more in the case of older fish	36+(P) – wrong section plane and part crystalline

Table 2. Mean, standard deviation, minimum, maximum and modal number of gillrakers by population depth zone groups. Subscripts a, b and c indicate groups that differ significantly (P<0.0001) based on ANOVA with post-hoc Tukey's test.

DFA groups	Mean	N	Standard Deviation	Minimum	Maximum	Mode
Keith Arm Shallow	45.27_a	325	2.145	38	52	45
Dease Arm Shallow	41.58_b	80	2.676	36	49	41, 44
Keith Arm Deep	39.89_c	190	2.404	35	49	39
Dease Arm Deep	39.52_c	211	2.558	30	47	41

Table 3. Discriminant function loadings for morphometric and meristic variables based on discriminant function analyses for a priori *population-depth zone based groups and hierarchical cluster analysis based groups. Characters with the highest loadings on axis 1 and 2 are shaded in grey.*

Variable	Between *a priori* population-depth zone based groups			Between hierarchical cluster analysis based groups	
	DF1	DF2	DF3	DF1	DF2
Morphometric					
POL	-.502	.096	-.184	.173	-.250
OOL	.193	.016	-.446	-.121	.068
PSL	.223	.266	-.337	.056	.114
TTL	.141	.430	-.278	.117	.287
DOL	.260	.377	.104	-.022	.274
LUL	.409	.361	.348	-.057	.440
ANL	.221	.137	.122	.075	.147
CPL	.810	-.313	-.228	-.265	.238
HDD	-.133	.298	.083	.023	.081
BDD	-.297	-.158	-.155	.107	-.367
CPD	.558	-.131	.455	-.195	.140
IOW	-.066	-.726	.169	.089	-.343
MXL	-.129	-.170	.023	.020	-.046
MXW	.076	.012	-.046	-.008	.083
PCL	-.279	.133	-.082	.205	-.086
PVL	-.123	-.175	.220	-.005	-.134
ADL	.104	.003	-.100	-.006	.059
GRL	.217	.375	.435	-.207	.255
LAL	.008	-.323	.163	.051	-.133
PMA	-.100	.300	-.175	.814	.431
Meristic					
LLS	.574	-.666	-.383	.813	-.564
DRC	.240	-.331	.725	.101	-.057
ARC	-.002	.642	.077	-.152	.278
PRC	.194	.450	-.432	.156	.183
VRC	.169	.001	.366	.070	.165
TGR	.692	.376	.176	.383	.767

Table 4. Cross validated classification matrix based on a priori population-depth zone groups. Percentages of individuals that correctly classified back to their own group are shaded grey.

DFA group	Predicted Group Membership (%)			
	Keith Arm Shallow	Keith Arm Deep	Dease Arm Shallow	Dease Arm Deep
Morphometric				
Keith Arm Shallow	98.4	.3	.6	.6
Keith Arm Deep	3.3	91.1	1.1	4.4
Dease Arm Shallow	5.6	4.2	69.0	21.1
Dease Arm Deep	.6	2.2	5.5	91.7
Meristic				
Keith Arm Shallow	95.1	.9	2.8	1.2
Keith Arm Deep	4.7	75.7	.6	18.9
Dease Arm Shallow	30.7	1.3	52.0	16.0
Dease Arm Deep	4.0	17.9	4.6	73.4

Table 5. Cross validated classification matrix based on assigned groups from hierarchical cluster analysis. Percentage of individuals that correctly classified back to their own group are shaded grey.

DFA group	Predicted Group Membership (%)		
	Cluster 1	Cluster 2	Cluster 3
Morphometric			
Cluster 1	84.0	5.0	11.0
Cluster 2	4.7	81.9	13.5
Cluster 3	1.2	5.5	93.3
Meristic			
Cluster 1	54.7	19.3	26.0
Cluster 2	15.5	80.8	3.6
Cluster 3	7.0	0.3	92.7

Table 6. Frequency of occurrence of prey items found in the stomach of deep- and shallow-water groups of cisco from Keith Arm and Dease Arms, Great Bear Lake, NT. Prey above and below the dashed line are from terrestrial and aquatic sources, respectively.

Order/species	Sub Order/ Family	Keith Arm		Dease Arm	
		Deep	Shallow	Deep	Shallow
Coleoptera		0.10			0.09
Psocoptera					0.27
Lepidoptera			0.07		0.09
Hymenoptera (adult)		0.10	0.20		
	Formicidae	0.10	0.03		
Megaloptera (adult)			0.13	0.10	
Hemiptera (adult)			0.07		
	Cicadellidae		0.07		
Trichoptera (adult)			0.77		
Diptera (adult)		0.50	0.63		0.09
	Nematocera		0.27		
	Brachycera	0.10	0.30		
Trichoptera (pupae/larvae)				0.20	0.45
Diptera (pupae)			0.03		
Diptera (larvae)	Orthocladiinae	0.10			
Amphipoda			0.03		
Copepoda			0.63		1.00
Ostracoda				0.20	0.09
Cladocera			0.07	0.50	0.55
Mysis diluviana		0.90	0.30	0.90	0.36
Pisidiidae				0.10	
Fish remains		0.10	0.17	0.30	0.64

Empty cells are equal to zero.

Table 7. Mean and standard deviation of significantly different fatty acids between shallow- and deep-water groups of cisco from Keith and Dease arms of Great Bear Lake.

	Keith Arm		Dease Arm	
	Shallow	**Deep**	**Shallow**	**Deep**
12:0	0.06 ± 0.07	0.16 ± 0.02	0.04 ± 0.01	0.16 ± 0.05
12:1			0.01 ± 0.01	0.004 ± 0.003
14:0	2.11 ± 0.69	3.04 ± 0.42	1.68 ± 0.53	3.12 ± 0.85
14:1n9			0.01 ± 0.003	0.031 ± 0.007
14:1n5			0.03 ± 0.007	0.07 ± 0.02
15:1n6			0.03 ± 0.014	0.016 ± 0.006
15:1n:8	0.01 ± 0.004	0.002 ± 0.002		
15:0 iso	0.51 ± 0.28	0.17 ± 0.06		
16:0	19.15 ± 1.4	16.54 ± 0.61	19.15 ± 0.86	16.03 ± 0.95
16:1Tn11	0.17 ± 0.04	0.12 ± 0.02	0.13 ± 0.03	0.09 ± 0.023
16:1n7	2.58 ± 1.18	5.33 ± 0.49	1.94 ± 0.67	5.67 ± 2.36
16:2n4	0.07 ± 0.04	0.12 ± 0.04	0.05 ± 0.026	0.25 ± 0.12
17:0	0.26 ± 0.03	0.20 ± 0.02	0.26 ± 0.029	0.19 ± 0.016
17:1	0.11 ± 0.03	0.20 ± 0.02	0.1 ± 0.02	0.2 ± 0.034
16:4n1	0.08 ± 0.04	0.06 ± 0.01	0.04 ± 0.017	0.08 ± 0.042
16:4n3			0.03 ± 0.007	0.14 ± 0.07
18:0	3.14 ± 0.37	2.38 ± 0.16	3.15 ± 0.36	2.24 ± 0.20
18:1n9t			0.06	0.04 ± 0.02
18:1n11			0.07 ± 0.37	0.03 ± 0.03
18:1n9c	8.59 ± 2.15	16.85 ± 1.68	7.4 ± 1.38	14.23 ± 1.54
18:1n7	2.82 ± 0.50	3.86 ± 0.29	2.72 ± 0.26	3.56 ± 0.19
18:1n5	0.22 ± 0.06	0.30 ± 0.06	0.19 ± 0.04	0.25 ± 0.03
18:2n4			0.08 ± 0.02	0.11 ± 0.02
18:3n6	0.14 ± 0.07	0.19 ± 0.04	0.15 ± 0.04	0.26 ± 0.07
18:3n3			1.87 ± 0.34	2.54 ± 0.55
18:3n4	0.09 ± 0.05	0.12 ± 0.02	0.07 ± 0.02	0.12 ± 0.02
18:4n1			0.02 ± 0.006	0.06 ± 0.02
18:4n3			0.90 ± 0.22	2.21 ± 0.85
20:1n9	0.99 ± 0.37	1.34 ± 0.30	0.71 ± 0.37	1.00 ± 0.22
20:1n11			0.02 ± 0.01	0.05 ± 0.02
20:5n3	5.13 ± 0.91	6.45 ± 0.82	5.6 ± 0.80	9.18 ± 0.86
21:5n3	0.12 ± 0.03	0.15 ± 0.01	0.13 ± 0.02	0.18 ± 0.03
22:2n6			0.40 ± 0.27	0.19 ± 0.07
22:3n6			0.46 ± 0.08	0.30 ± 0.05
22:4n3			1.27 ± 0.59	0.59 ± 0.26
22:5n6	2.81 ± 0.58	1.84 ± 0.20	3.35 ± 0.33	1.68 ± 0.26
22:5n3c	2.87 ± 0.34	2.49 ± 0.20	3.43 ± 0.29	2.14 ± 0.29
22:6n3	25.76 ± 5.91	15.98 ± 2.84	29.12 ± 13	18.23 ± 4.67
24:1n9	0.60 ± 0.21	0.41 ± 0.08		

Table 8. Comparison of mean gillraker counts from Great Bear Lake groups with C. zenithicus *and* C. artedi *in other large proglacial lakes.*

Species/morph	Lake	Total Gillrakers (mean)	Source
C. zenthicus	Superior	40.7, 41.9	1, 2
	Nipigon	34.9, 36.7, 30-51*	1, 2, 3
	Great Slave	41.6, 35-45*	2, 4
Keith Arm - Deep	Great Bear	39.9	
Dease Arm Deep	Great Bear	39.5	
C. artedi	Average over multiple North American lakes	50.1	2
C. artedi - lacustrine	Great Slave Lake	46-51+*	4
C. artedi - adfluvial	Great Slave Lake	41-45*	4
C. artedi - big eye	Great Slave Lake	35-45*	4
Keith Arm - shallow	Great Bear Lake	45.3	
Dease Arm- shallow	Great Bear Lake	41.6	

[1] Murray 2006; [2] Steinhilber et al. 2002; [3] Turgeon et al. 1999; [4] Muir et al. 2011
*represents range of values

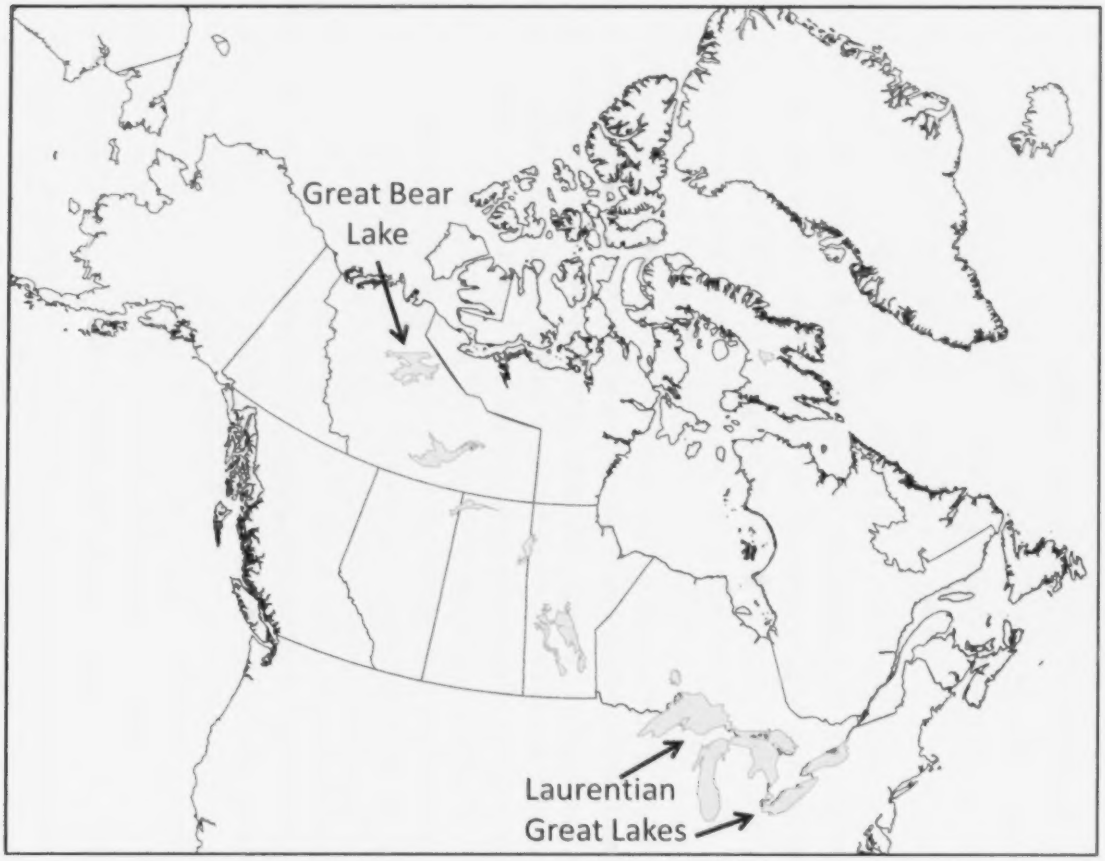

Figure 1. Map of Canada and Alaska showing North American large remnant pro-glacial lakes. Great Bear Lake and the Laurentian Great Lakes (referred to in the text) are indicated.

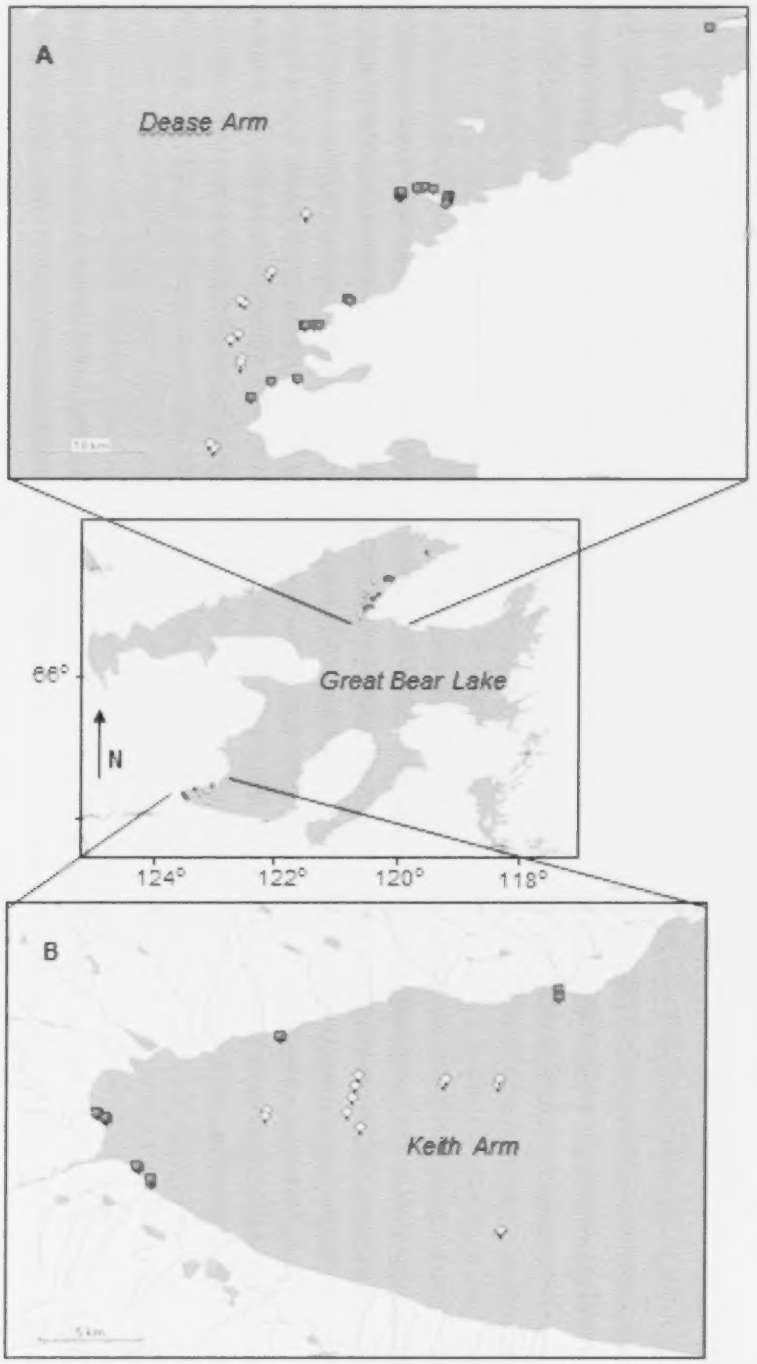

Figure 2. Map of Great Bear Lake showing locations where gillnets were set in A) Dease Arm 2010 and B) Keith Arm 2007 and 2008. Nets set in less than 50 m depth are shown in red, while nets set in 50–100 m depth are shown in white. Other arms of the lake include Smith, McTavish and McVicar (clockwise from left to right).

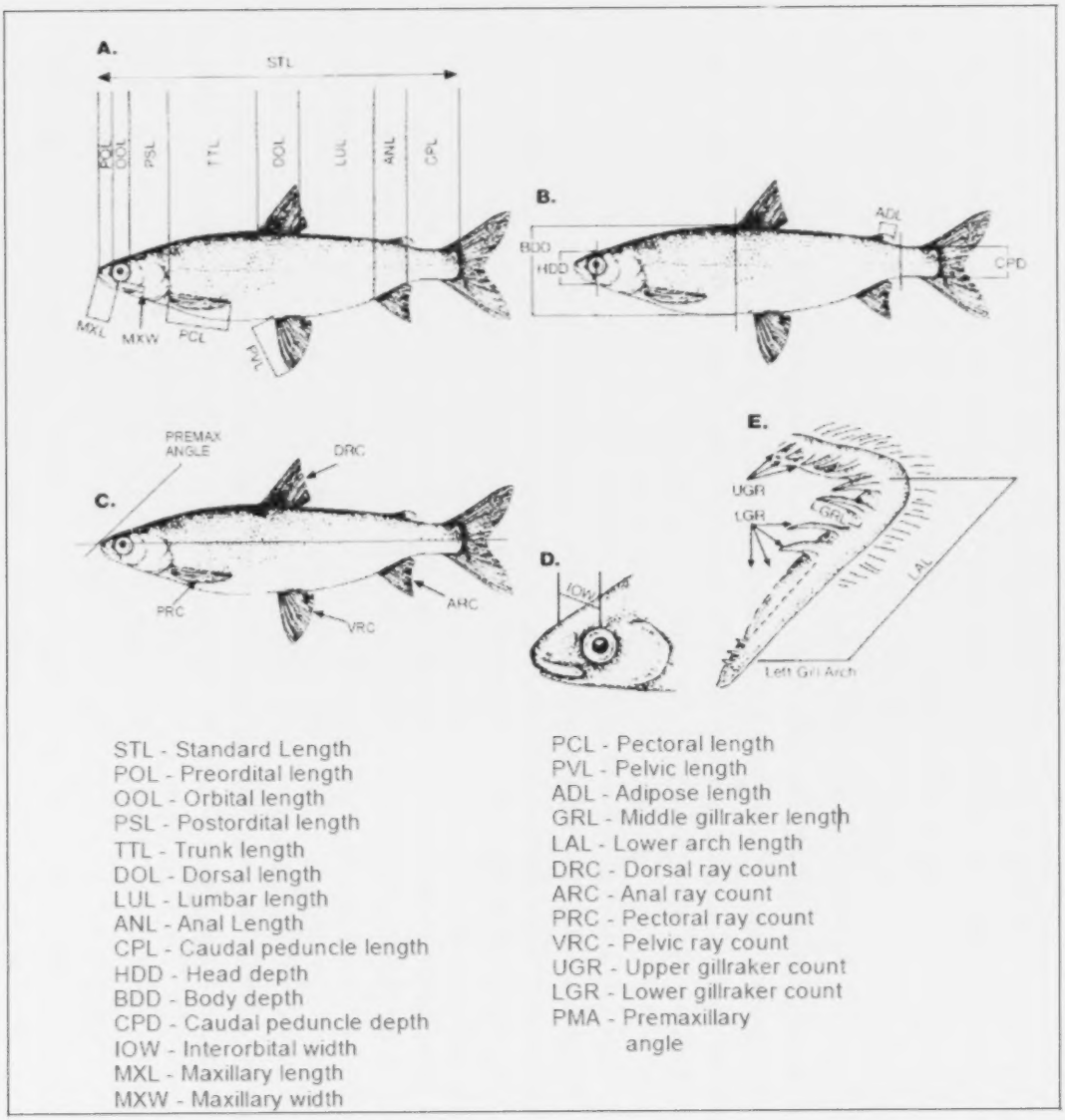

Figure 3. Morphometric and meristic characteristics included in this study after Vuorinen et al. (1993).

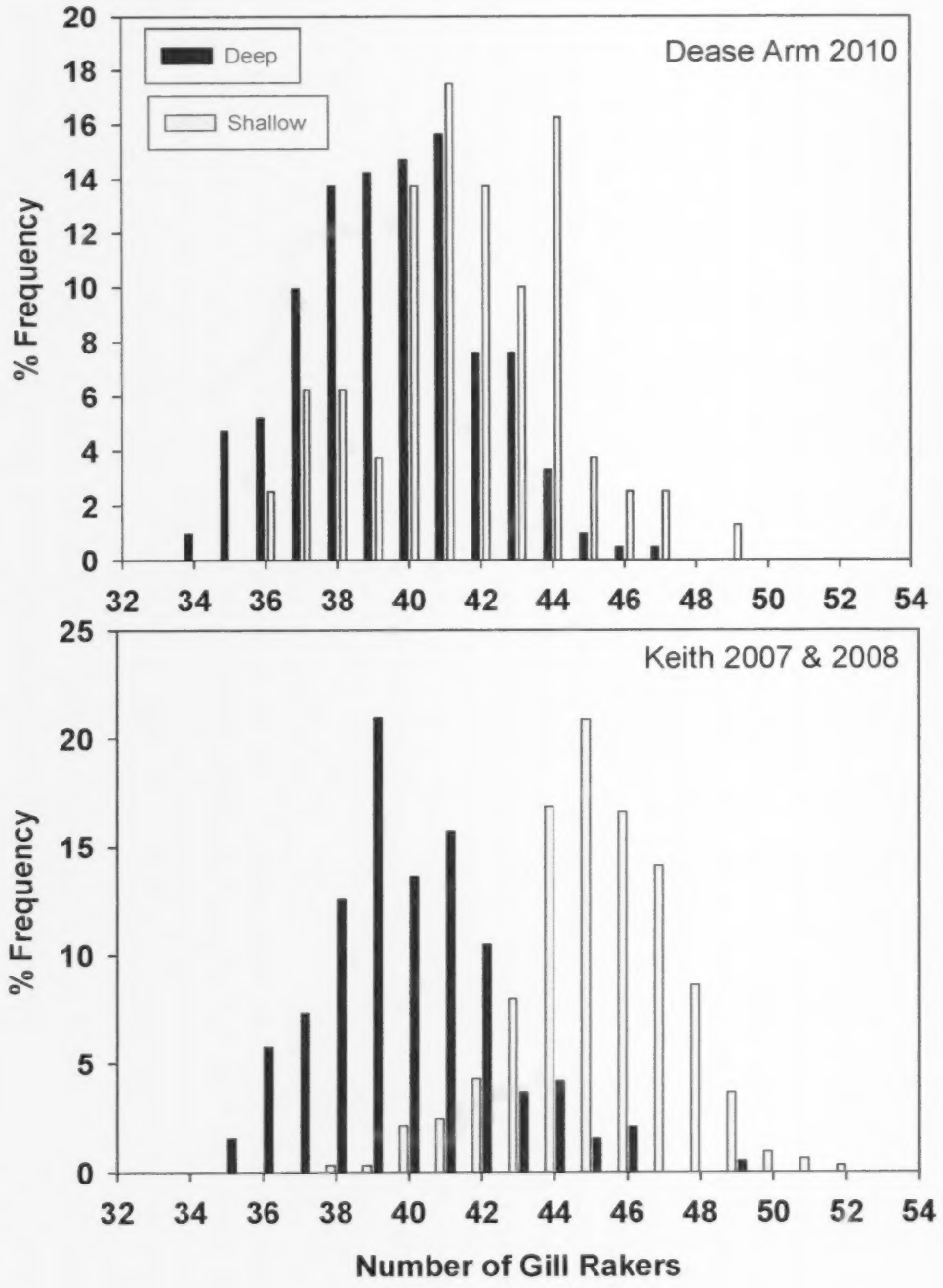

Figure 4. Frequency of gillrakers by population and depth zone.

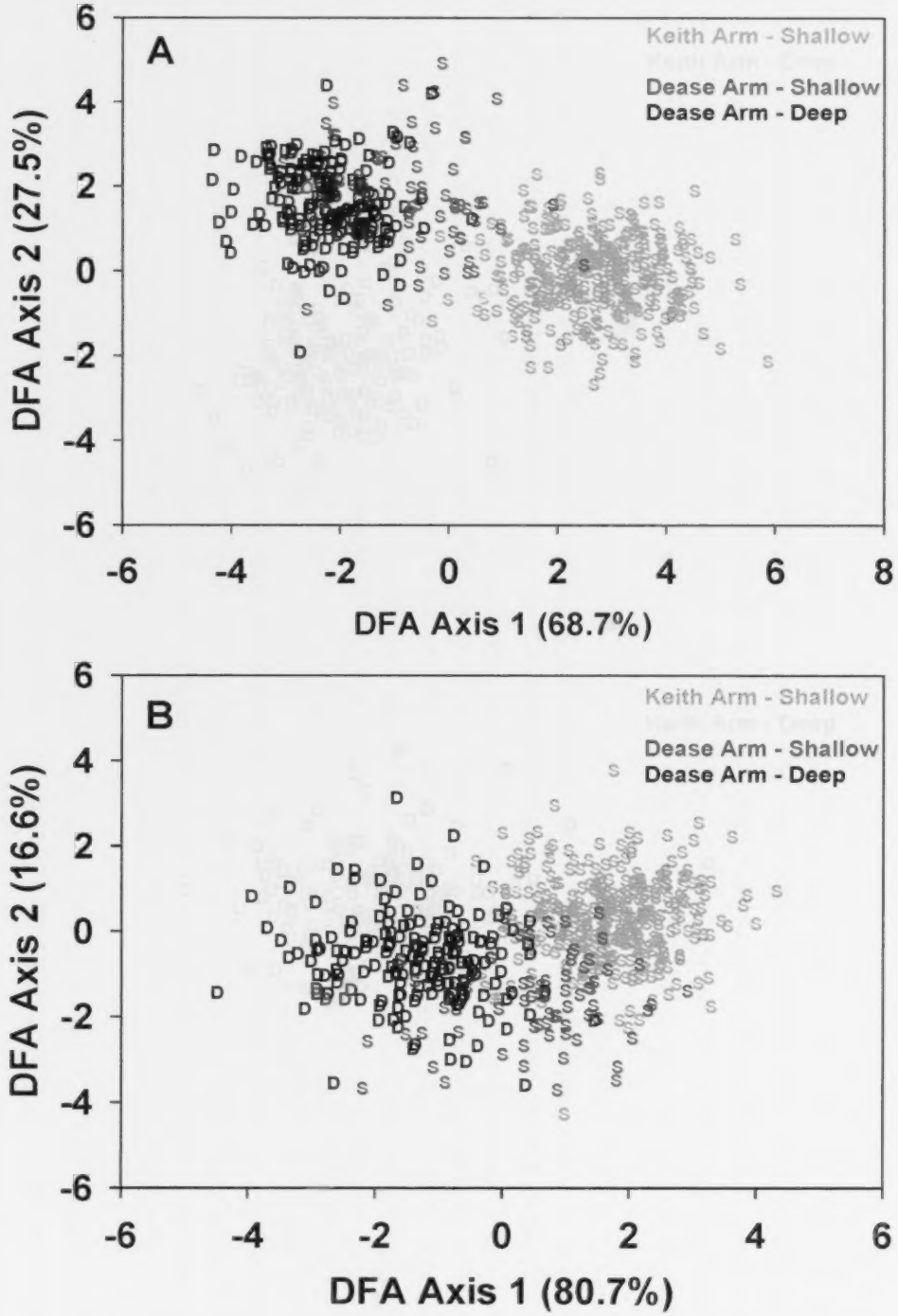

Figure 5. Discriminant function scores by population-depth zone groupings based on A) morphometric characters and B) meristic characters.

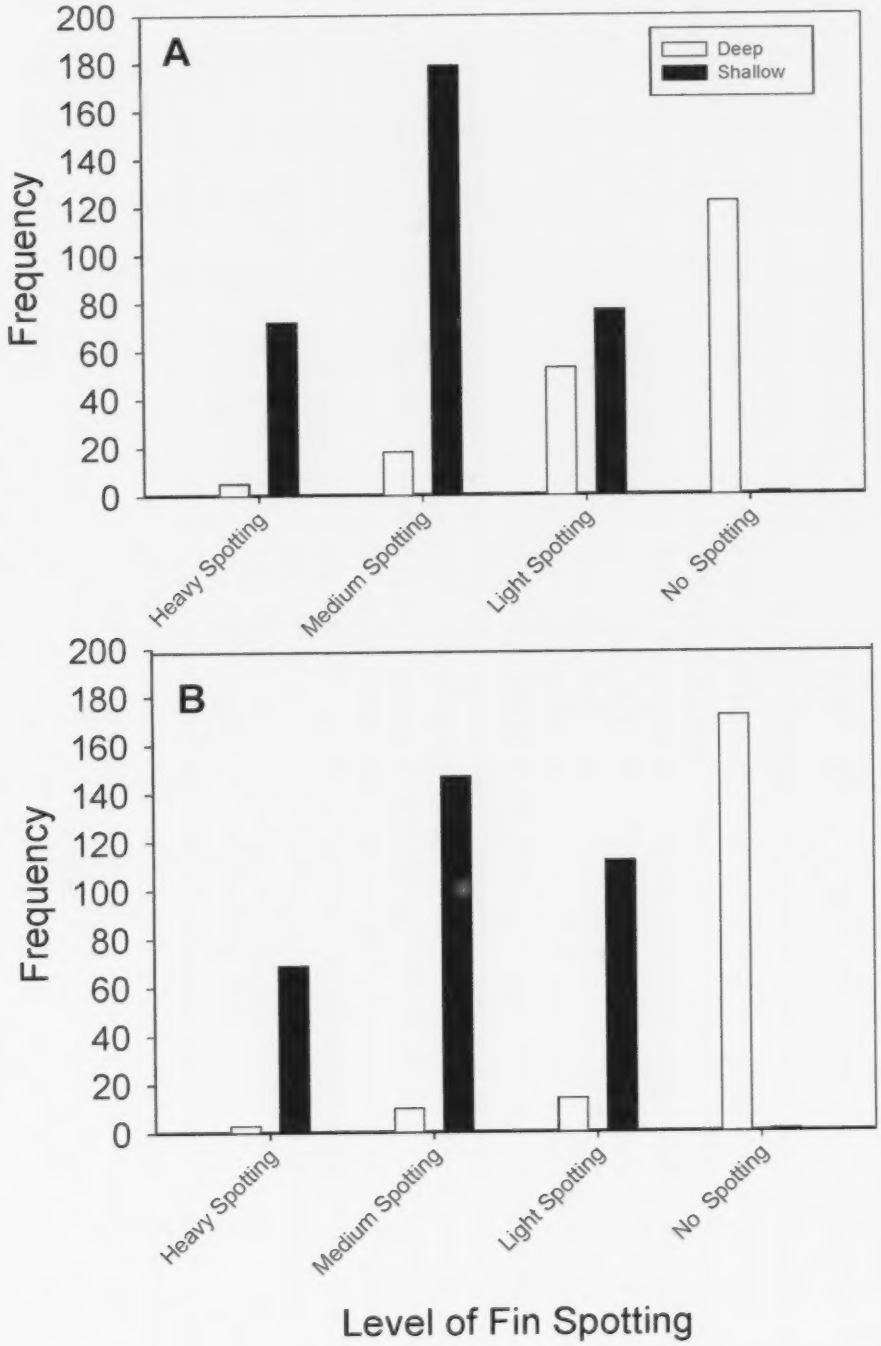

Figure 6. Level of A) pectoral and B) pelvic fin spotting in deep and shallow cisco morphs from Keith Arm.

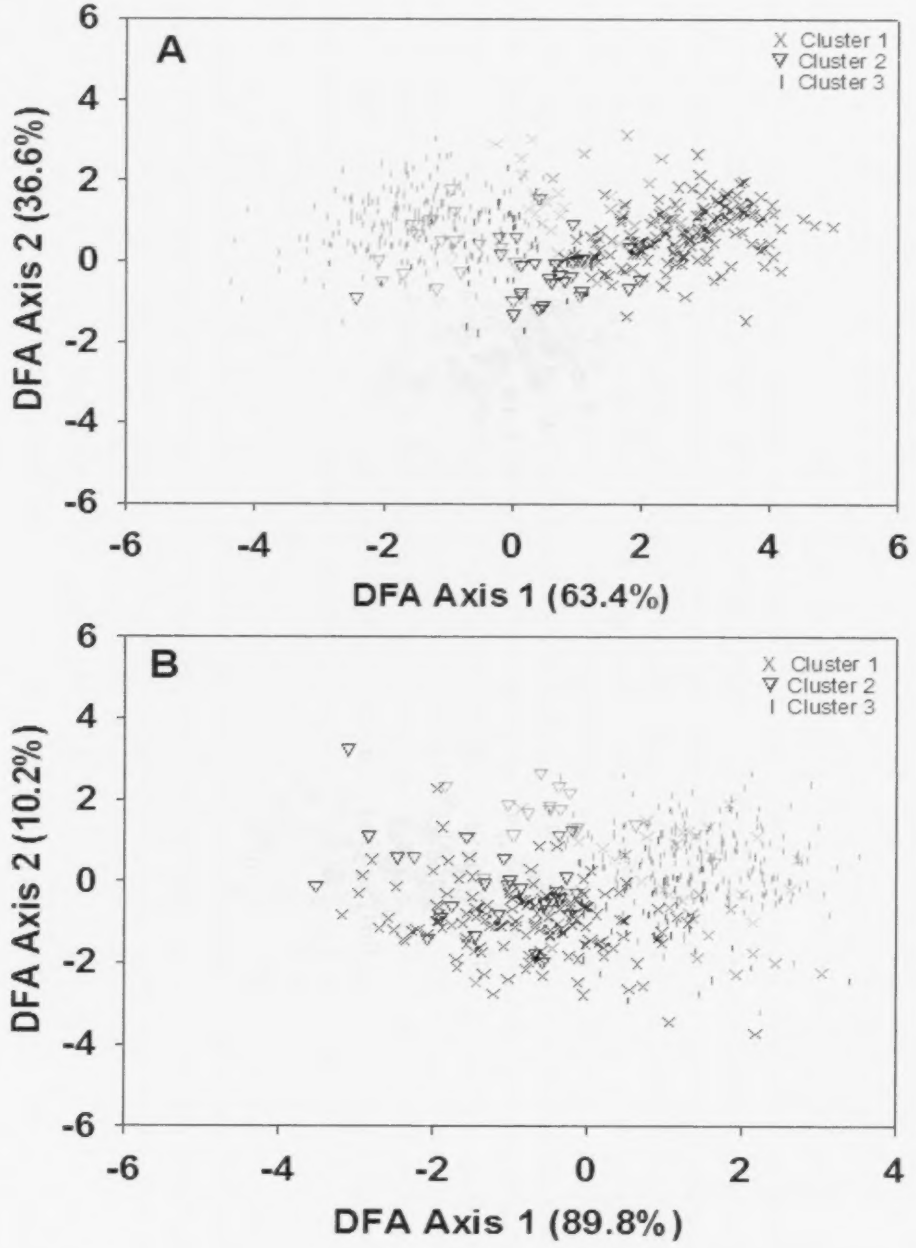

Figure 7. Discriminant function scores by cluster analysis-based groupings based on A) morphometric characters and B) meristic characters. Population-depth zone information is overlaid using the following symbols: Keith Arm - shallow = solid circles, Keith Arm - deep = open circles, Dease Arm – shallow = solid triangles, Dease Arm – deep = open triangles.

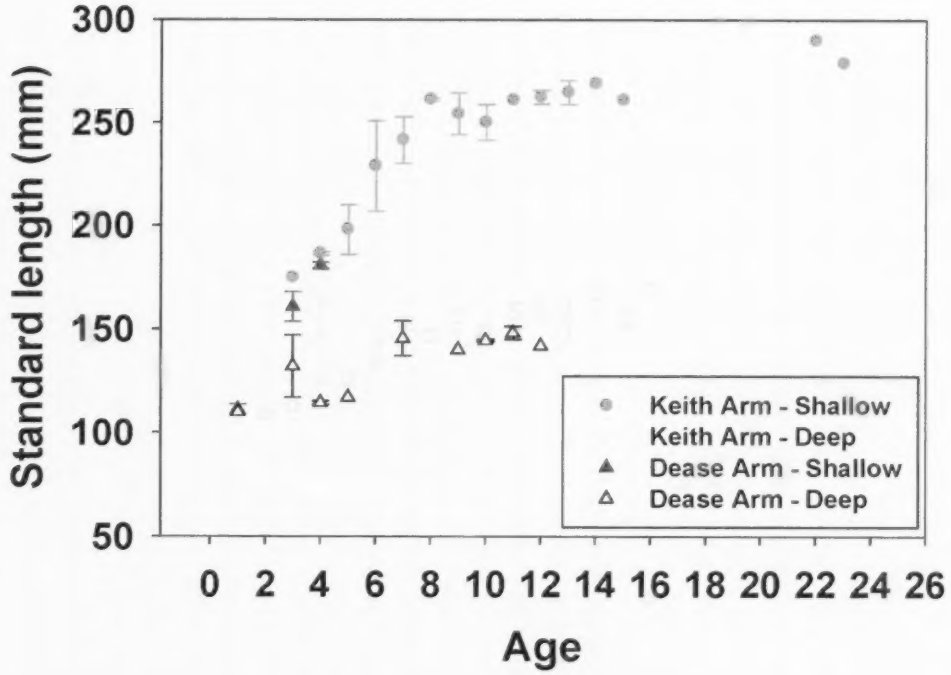

Figure 8. Mean size at age (± 1 standard error) by population-depth zone groups.

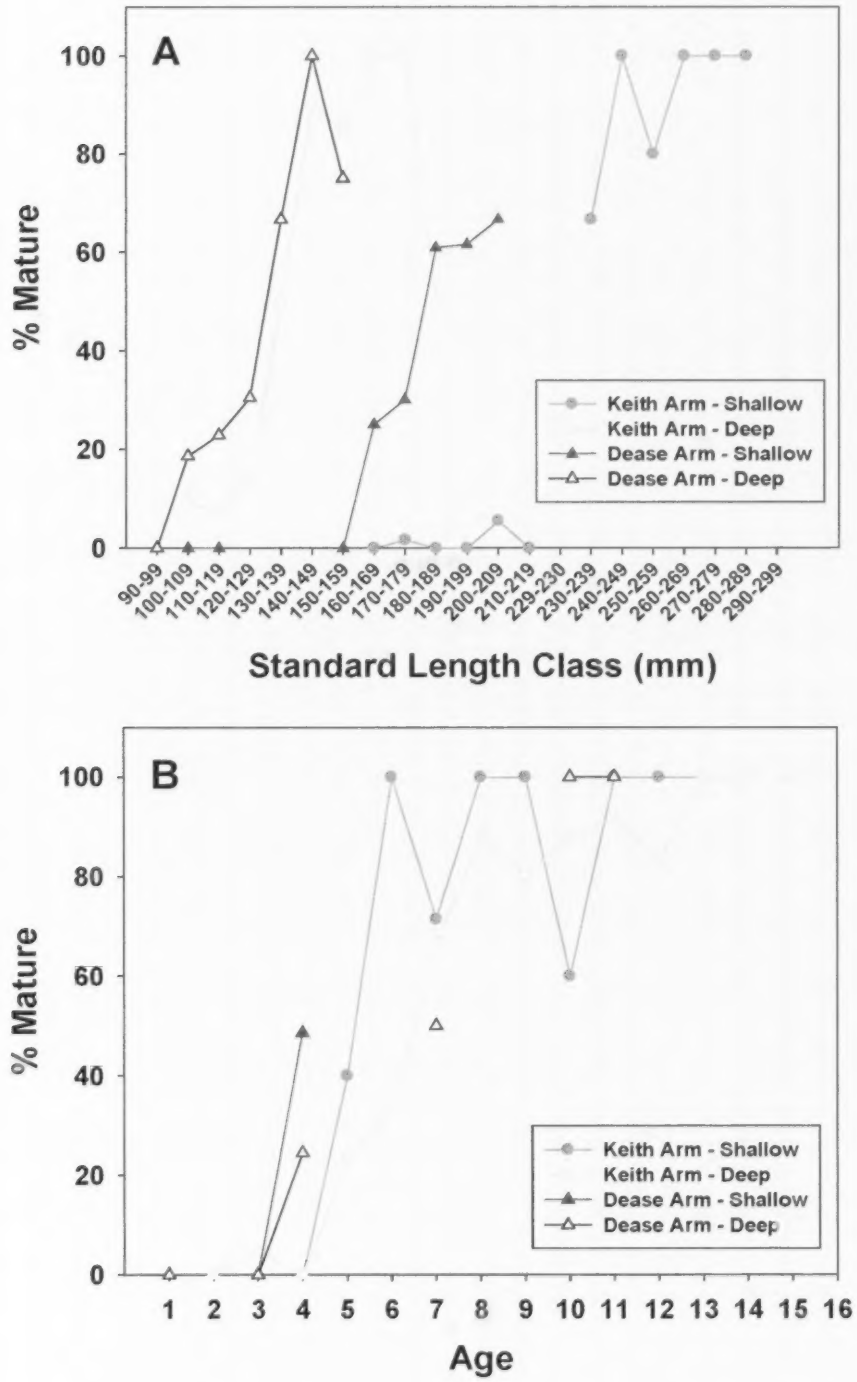

Figure 9. Percentage of mature individuals by A) size class and B) age class for each population-depth zone group. Data were not included for cases where n=1.

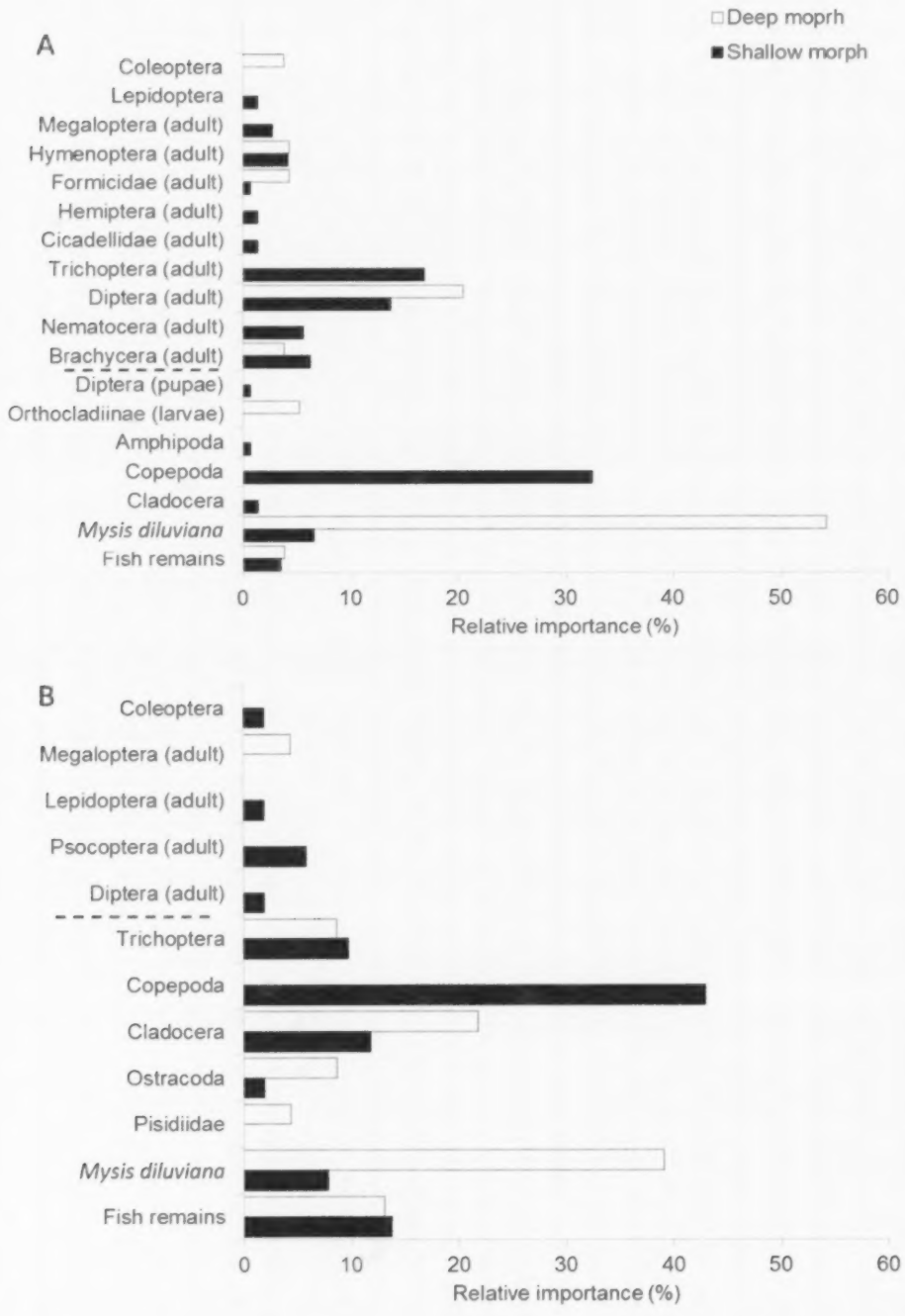

Figure 10. Relative importance (%) of 18 prey items to the diet of deep-water and shallow-water groups of cisco in the Keith Arm (A) and Dease Arm (B) of Great Bear Lake, NT. Prey above and below the dashed line are from terrestrial and aquatic sources, respectively.

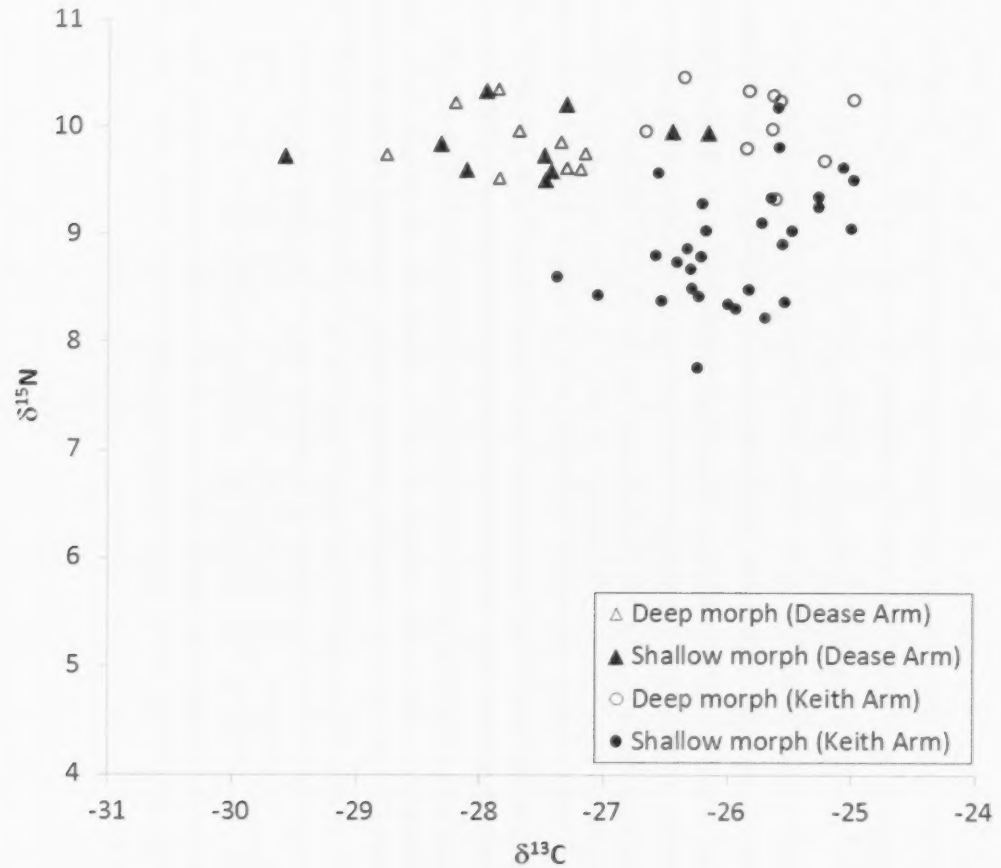

Figure 11. $\delta^{13}C$ and $\delta^{15}N$ of deep- and shallow-water groups of cisco from Keith and Dease arms of Great Bear Lake, NT.

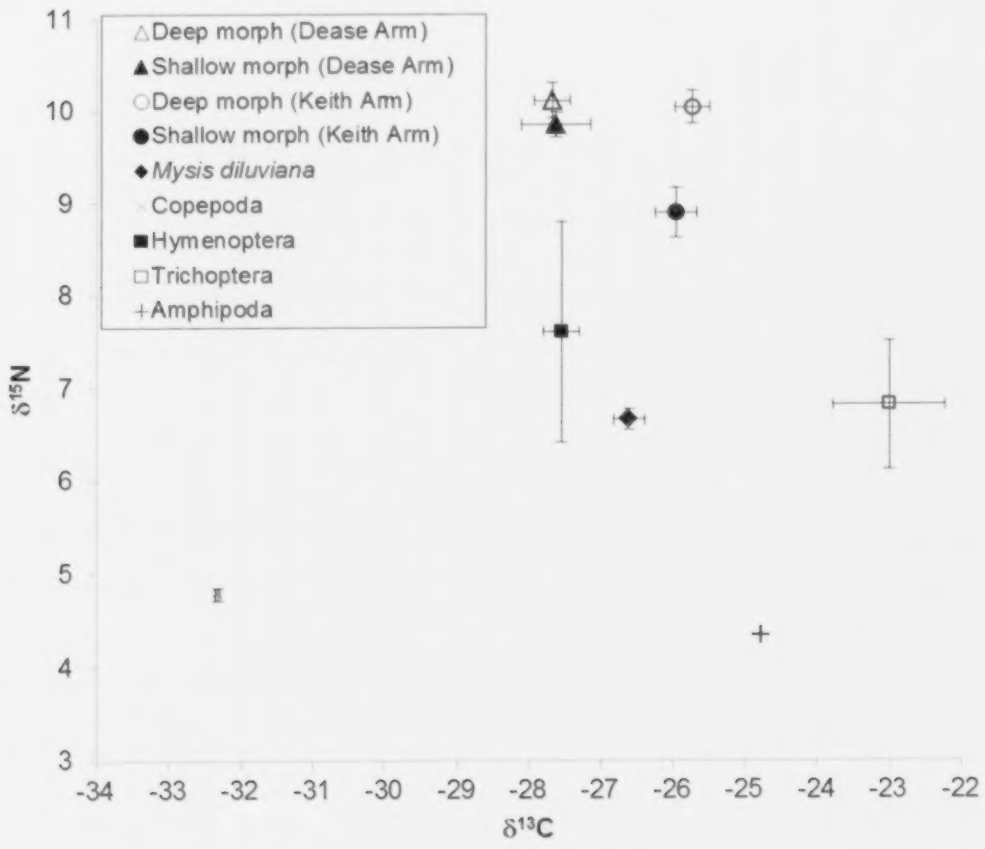

Figure 12. Mean and standard deviation of $\delta^{13}C$ and $\delta^{15}N$ of deep- and shallow-water groups of cisco and selected invertebrates from Great Bear Lake, NT.

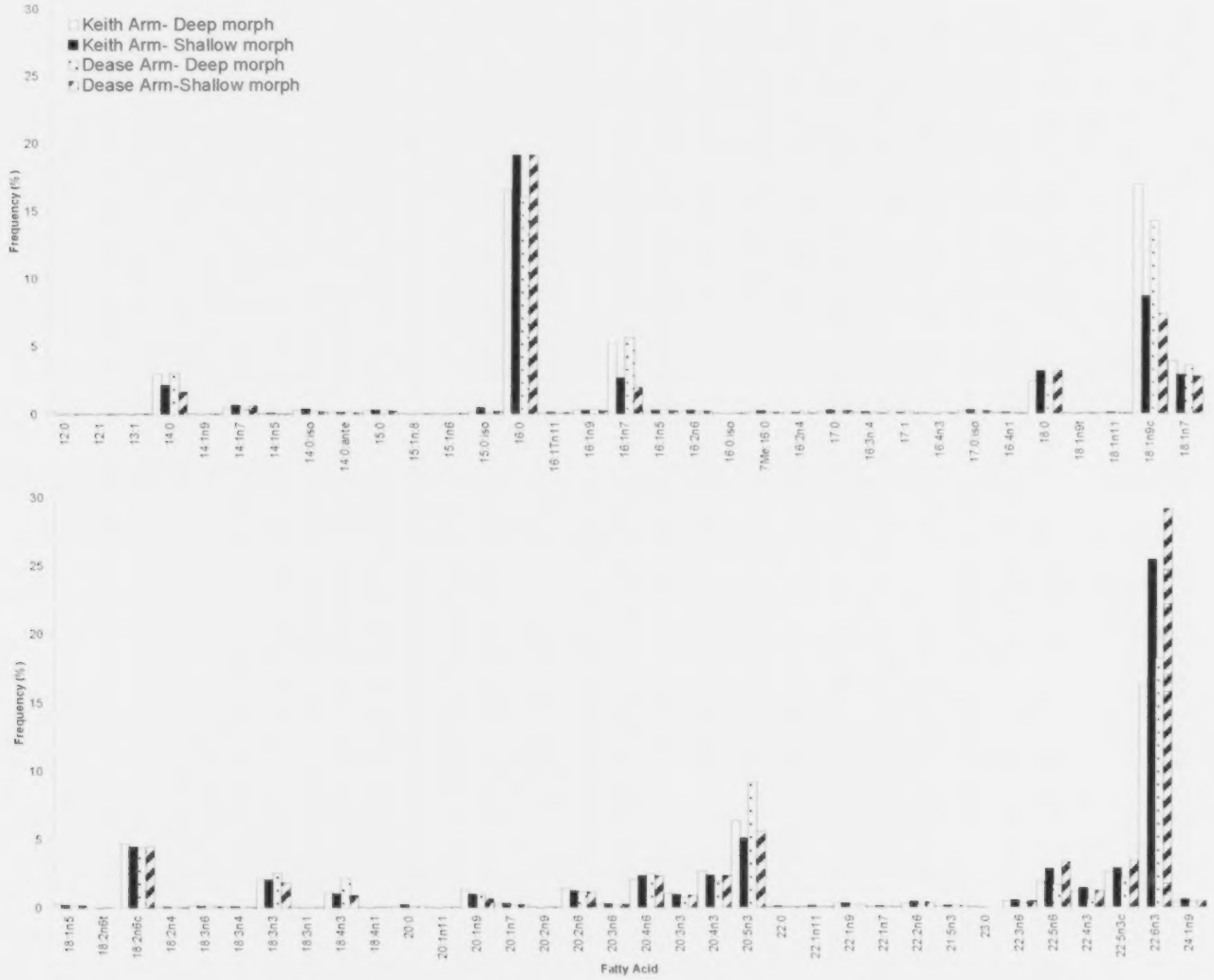

Figure 13. Profiles of 67 fatty acids from deep- and shallow-water groups of cisco from Keith and Dease arms of Great Bear Lake, NT.

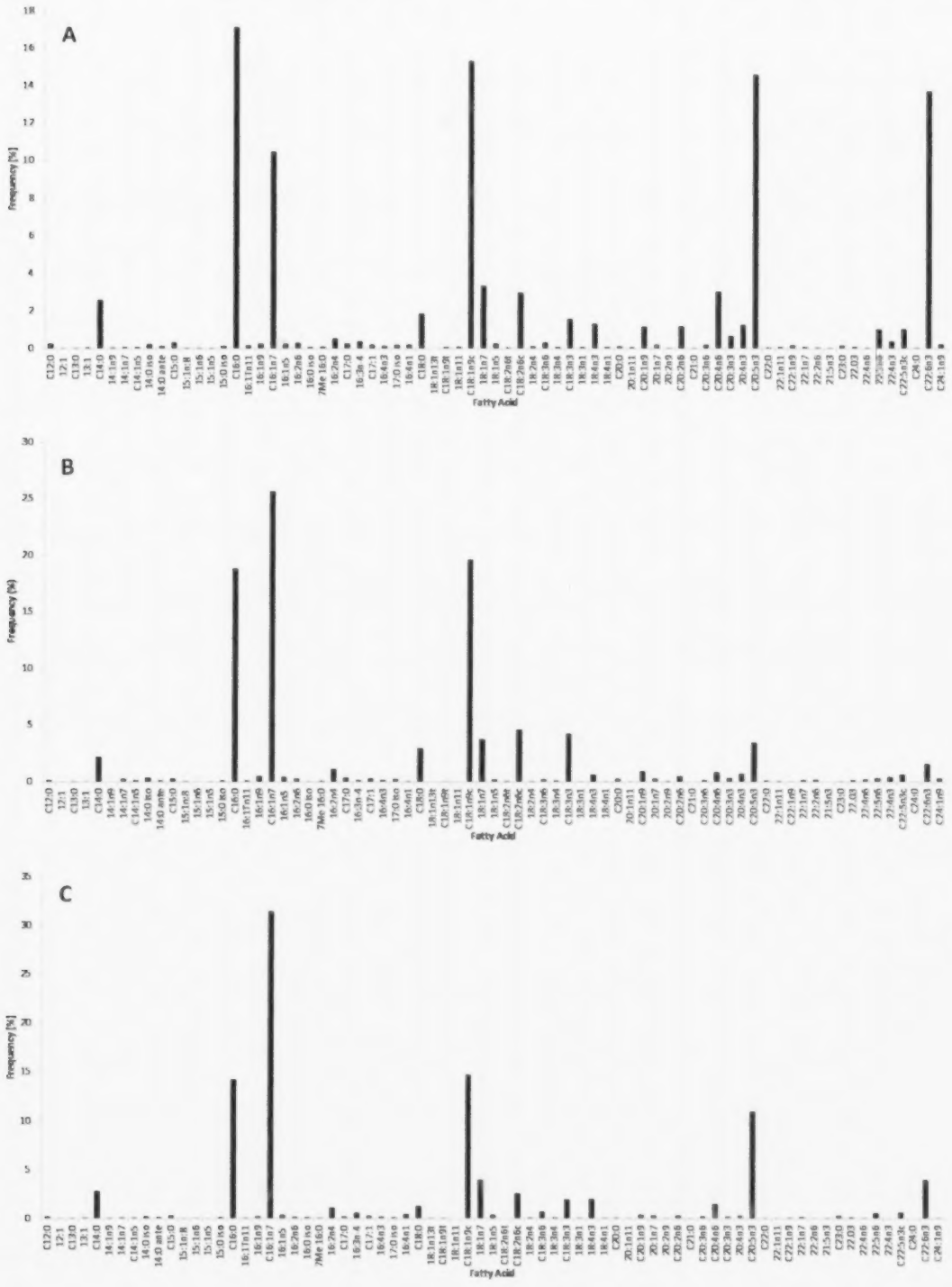

Figure 14. Fatty acid profile of Mysis diluviana (A), Trichoptera (B) and Amphipoda (C) from Great Bear Lake, NT.

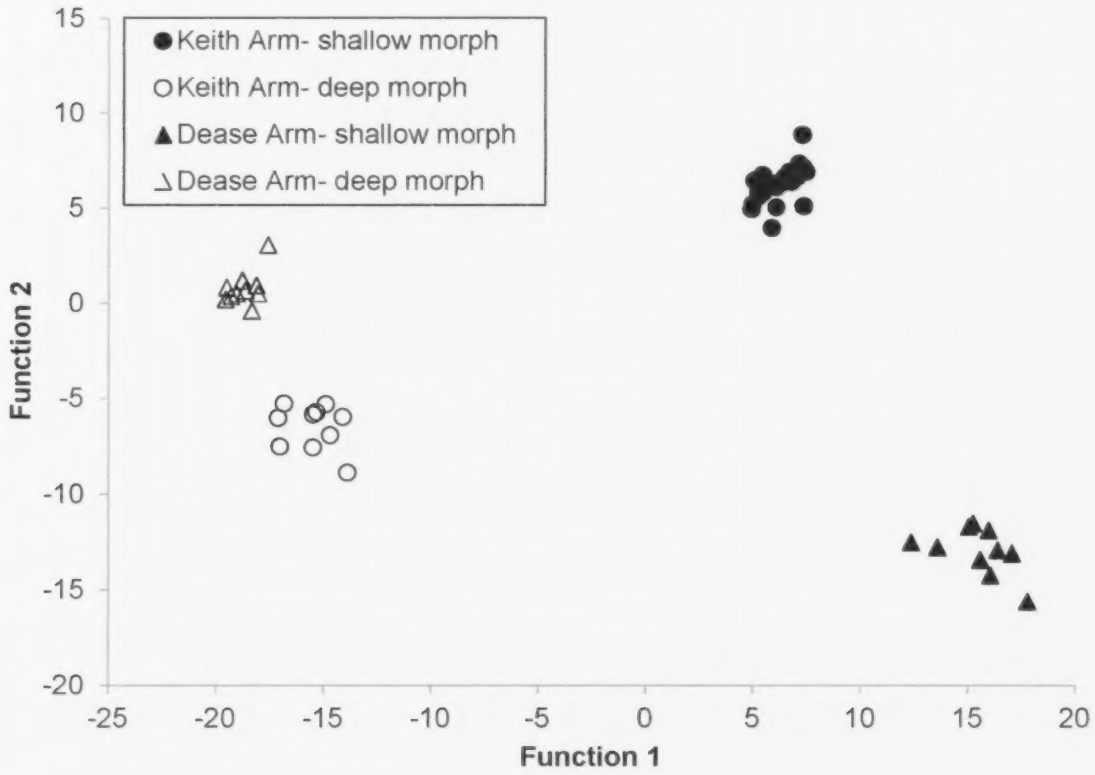

Figure 15. Discriminant function scores of fatty acids among shallow- and deep-water groups of cisco from Keith Arm of Great Bear Lake, NT.